National Research Council Canada
Conseil national de recherches Canada

NRC · CNRC

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

The *Canadian Journal of Fisheries and Aquatic Sciences* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, *Journal of the Biological Board of Canada* 1934–37, and *Journal of the Fisheries Research Board of Canada* 1938–79. The *Journal* is published by the National Research Council of Canada in cooperation with the Department of Fisheries and Oceans.

The *Journal* is issued monthly to form annual volumes of twelve numbers plus Supplements.

Editorial Policy

The *Journal* publishes original research articles, critical reviews, perspectives (essays of opinion or hypothesis), and comments. Papers may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and they should lead to identifiable conclusions or syntheses, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of fisheries and aquatic sciences. They should demonstrate clearly a contribution to knowledge beyond the confirmation state. Originality should relate to more than the particular (a certain year, place, taxon, or chemical compound) such that existing understanding is reformulated or extended.

It would assist the Editors if prospective authors identified briefly by covering letter (a) aspects of their papers that meet the foregoing objectives, (b) potential referees, and (c) other manuscripts contemplated or in press containing the same or similar information.

Submissions in English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor. The National Research Council of Canada accepts no responsibility for statements or opinions expressed by a contributor. Acceptance of an advertisement, announcement, or other material does not imply endorsement by either the *Journal*'s Editors or the National Research Council. The use of proprietary names does not imply endorsement of the product or company.

Guides

A guide for authors appears in the first issue of each volume and is available free from the *Journal*.

Microfilm

Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, USA.

©National Research Council of Canada 1994. World rights reserved.

The National Research Council of Canada grants permission* to individuals who wish to quote short excerpts and reproduce figures, tables, or photographs from articles in this journal, provided that the source of such material is fully acknowledged. As a courtesy the consent of authors of such material should be obtained.

Authorization to photocopy items for internal or personal use, or the internal or personal use of specific clients, is granted by the National Research Council of Canada for libraries and other users registered with the Copyright Clearance Center (CCC) Transactional Reporting Service, provided that the base fee of $3.00 per copy is paid directly to CCC, 21 Congress Street, Salem, MA 01970, USA. 0706-652X/94 $3.00 + 0.00.

*The above permission does not extend to other kinds of copying, such as copying for general distribution, for advertising, or promotional purposes, for creating new collective works, or for resale. For such copying, arrangements must be made with the National Research Council of Canada.

U.S. second-class postage paid at Champlain, N.Y., and at additional mailing offices. U.S. POSTMASTER: Send address changes to *Canadian Journal of Fisheries and Aquatic Sciences*, c/o USACAN Media Distribution Center, P.O. Box 2888, Plattsburg, NY 12901, USA.

Design: Ludvic Saleh & Associates, Ottawa
Conception graphique : Ludvic Saleh & Associates, Ottawa

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937 et *Journal de l'office des recherches sur les pêcheries du Canada* 1938–1979. Le *Journal* est publié par le Conseil national de recherches du Canada en collaboration avec le ministère des Pêches et des Océans.

Le *Journal* paraît tous les mois, formant ainsi un volume de douze numéros, et offre en plus jusqu'à deux suppléments par année.

Politique de rédaction

Le *Journal* publie des articles fondés sur une recherche originale, des critiques, des essais portant sur une opinion ou une hypothèse (perspectives) et des commentaires. Les textes peuvent avoir trait aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influent sur les systèmes de production aquatique. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverses façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel des connaissances et perceptions dans une discipline donnée des sciences aquatiques. Ils doivent clairement démontrer qu'ils contribuent aux connaissances en faisant plus que corroborer des faits. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donné) et tenir à une épuration ou à une reformulation des connaissances actuelles.

Les auteurs éventuels aideraient les rédacteurs s'ils identifiaient brièvement, dans une lettre d'accompagnement a) les aspects de leurs textes qui répondent particulièrement aux objectifs indiqués ci-dessus, b) des arbitres possibles et c) d'autres manuscrits envisagés ou sous presse, dont la teneur est identique ou se rapproche de celui qui est soumis.

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à.-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le Conseil national de recherches du Canada ne se tient en aucune façon responsable des opinions exprimées par un collaborateur ou des déclarations que pourrait faire ce dernier. La publication d'annonces publicitaires, d'avis et autres n'implique pas l'endossement de leur contenu par les directeurs du *Journal* ou du Conseil national de recherches du Canada. L'utilisation des noms de marques de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique.

Guides

Le guide des auteurs paraît dans la première livraison de chaque volume et est offert gratuitement par le *Journal*.

Microfilms

On peut acheter sur microfilms de 16 ou 35 mm tous les numéros publiés depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, É.-U.

©Conseil national de recherches du Canada 1994. Tous droits réservés.

Le Conseil national de recherches du Canada accorde aux particuliers la permission* de citer de brefs extraits et de reproduire des figures, des tableaux ou des photos dans les articles du *Journal*, à la condition que la source soit indiquée explicitement. Dans ce cas, il convient, par courtoisie, d'obtenir le consentement des auteurs.

Le Conseil national de recherches du Canada autorise les bibliothèques et autres utilisateurs inscrits au Copyright Clearance Center (CCC) Transactional Reporting Service à photocopier les documents destinés à un usage interne ou personnel, ou à l'usage interne ou personnel de clients particuliers, à la condition que le tarif de base de 3 $ par copie soit payé directement au CCC, 21 Congress Street, Salem, MA 01970, USA. 0706-652X/94 3,00 $ + 0.00.

*La présente permission ne s'applique pas à d'autres genres de reproduction, notamment la reproduction en vue d'une distribution générale, à des fins de publicité ou de promotion, pour la création de nouveaux travaux collectifs, ou pour la revente. Dans ces cas, il faut prendre les dispositions qui s'imposent en communiquant avec le Conseil national de recherches du Canada.

Courrier de seconde classe des É.-U. payé à Champlain, N.Y., et d'autres centres de courrier. MAÎTRE DE POSTE des É.-U. : Faire parvenir les corrections d'adresse à *Journal canadien des sciences halieutiques et aquatiques*, a/s du Service de distribution médias USACAN Inc., C.P. 2888, Plattsburg, NY 12901, É.-U.

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 51, No. 12, December 1994 **Volume 51, nº 12, décembre 1994**

D.G. Cook — *Editor/Rédacteur*
M.M. Milne — *Assistant to the Editor/Adjointe au rédacteur*
P.E.K. Symons — *Consulting Editor/Rédacteur-conseil (Victoria, B.C.)*
N. Moir — *Consulting Editor/Rédacteur-conseil (Nepean, Ont.)*

Editorial Board/Conseil de rédaction

L.M. Dickie — *DFO/MPO, Dartmouth (Advisor/Conseiller)*
G.S. Jamieson — *DFO/MPO, Nanaimo (Associate Editor/Rédacteur associé)*
J.R.M. Kelso — *DFO/MPO, Sault Ste. Marie (Associate Editor/Rédacteur associé)*
J.D. Neilson — *DFO/MPO, St. Andrews (Associate Editor/Rédacteur associé)*
L.S. Parsons — *DFO/MPO, Ottawa (Advisor/Conseiller)*
R.M. Peterman — *Simon Fraser University (Advisor/Conseiller)*
J.C. Roff — *University of Guelph (Advisor/Conseiller)*
P. Schwinghamer — *DFO/MPO, St. John's (Deputy Editor/Rédacteur adjoint)*
C.J. Walters — *University of British Columbia (Advisor/Conseiller)*
W.G. Warren — *DFO/MPO, St. John's (Associate Editor/Rédacteur associé)*
N.H.F. Watson — *DFO/MPO, Halifax (Associate Editor/Rédacteur associé)*

Research Journal/Revues scientifiques

Bruce P. Dancik — *Editor-in-chief/Directeur général*
Iain E.P. Taylor — *Assistant Editor-in-chief/Directeur général adjoint*

Publishing Department/Service de publication

Aldyth Holmes — *Director/Directrice*
Paul McClymont — *Business Manager/Gestionnaire des affaires*
Susan R. Strahlendorf — *Production Manager/Gestionnaire de la production*
Mike Boroczki — *Senior Publication Officer/Agent principal de publication*
Michael Sharpe — *Publication Officer/Agent de publication (613-993-0994)*
Ginette Fortier — *Publication Officer (French manuscripts)/Agent de publications (manuscrits français) (613-993-9117)*
Hoda Jabbour — *Advertising/Annonces publicitaires (613-993-9085)*
Eileen Fink — *Reprints/Tirés à part (613-993-09151)*

Editorial Office:
Research Journals
National Research Council of Canada
Ottawa, ON K1A 0R6
Canada
Telephone (613) 993-2209
FAX (613) 952-7656
E-mail: reserach.journals@nrc.ca

Bureau de rédaction :
Revues scientifiques
Conseil national de recherches du Canada
Ottawa ON K1A 0R6
Canada
Téléphone (613) 993-2209
Télécopieur (613) 952-7656
Courrier électronique : research.journals@nrc.ca

The *Journal* is abstracted or indexed in:/Le *Journal* est résumé ou signalé dans :

Aquatic Sciences and Fisheries Abstracts, Biological Abstracts, Biological & Agricultural Index, Chemical Abstracts, Current Awareness in Biological Sciences, Current Contents, FAO Freshwater and Aquaculture Contents Tables, FAO Marine Science Contents Tables, Geo Abstracts, GEOBASE, Meteorological and Geoastrophysical Abstracts, Oceanic Abstracts, and *Science Citation Index*

Recent Developments in the Quantitative Analysis of Fisheries Data

Laura J. Richards

Department of Fisheries and Oceans, Biological Sciences Branch, Pacific Biological Station, Nanaimo, BC V9R 5K6, Canada

and Bernard A. Megrey

NOAA, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA

According to FAO statistics, the world fisheries catch peaked in 1989 at 100.3 million tonnes and declined to 98.1 million tonnes in 1992, the most recent year for which data are available. The limit to "wild" marine fisheries production has probably been reached (FAO 1994), where a relatively constant recent catch reflects increased fishing effort as stock abundances decline. Within the United States, 40% of the 163 fish stocks with known status are overexploited and an additional 45% are fully utilized (NMFS 1993). The Atlantic groundfish fishery collapse has been attributed to overfishing (Anthony 1993; Hutchings and Myers 1994).

In the face of diminishing resources, stock assessments are becoming more urgent and more controversial. Stock assessments interpret fishery resource status on the basis of data compiled from both fishers and fish populations. This information is then used to determine biologically reasonable harvest strategies. The global fisheries situation underscores the need for accuracy. How can harvests of marine fish species be sustained? What are the risks associated with different harvest options? How do multifleet and multispecies fisheries interact? How can stock status be determined from biased or incomplete data? Which additional data sources might provide valuable clues to stock status?

In 1993, we organized a symposium on new approaches in quantitative analysis that addressed these and other questions related to marine fisheries stock assessment. The overall focus was intentionally broad, recognizing the diversity of data used in current assessments and their associated problems. North American approaches to marine fisheries stock assessment tend to differ by geographic region (Rosenberg and Restrepo 1994). Thus, we invited participation from the major fisheries agencies on the Atlantic and Pacific coasts of North America. We hoped to stimulate discussion by providing a cross section of ideas and methodologies.

The symposium was convened on September 1, 1993, at the 123rd annual meeting of the American Fisheries Society in Portland, Oregon. Various talks dealt with specific inputs of assessment models, different modeling approaches, how to forecast yields, how to assign risks to potential harvest strategies, and how to communicate the results. The following eight papers provide a sample of the 20 symposium presentations. Other contributions (Quinn and Szarzi 1993; Schnute and Richards 1994; Jacobson and MacCall 1995) have been published elsewhere.

Current Directions in Stock Assessment

Tools to address the stock assessment challenge have improved markedly over the last decade, in terms of both technology (e.g., computer hardware and software) and statistical methodology. One theme that emerged from the symposium was how these methodologies provide new avenues for data visualization. In particular, graphical software tools facilitate exploratory analysis of large and complex data sets. This increased sophistication enables users to focus on interpretation and hypothesis testing rather than on the mechanics of specific analyses. For example, graphical analyses of spatial data are now integral to the process of examining movements of fish and fisheries for clues to stock distribution and localized abundance (e.g., Kleiber and Hampton 1994).

Faster computer processing speeds contribute to the application of modern statistical methodologies. For example, the sampling/importance resampling algorithm is one recently developed procedure for estimating posterior distributions of important quantities including stock biomass (McAllister et al. 1994). Such statistical procedures support the trend to evaluating the uncertainty associated with scientific management advice (Rosenberg et al. 1993; Smith et al. 1993). Most symposium presentations involved some form of simulation analysis. For example, Quinn and Szarzi (1993), Megrey et al. (1994), and Sampson (1994) used simulation analysis to explore the consequences of alternative harvest scenarios.

Work is continuing to improve our understanding of basic population processes, including growth, survival (Thompson 1994), recruitment (Jacobson and MacCall 1995), and migration (Kleiber and Hampton 1994). However, symposium speakers generally recognized that complete modern assessments must reach beyond traditional treatments of fisheries and fish populations. For example, oceanographic variables are now examined routinely for additional clues to fish abundance fluctuations (e.g., Collie and Spencer 1994; Jacobson and MacCall 1995). Some analyses are only possible because of new technologies for data collection and dissemination. A wide variety of data bases can be accessed on CD-ROM or via Internet. These data bases provide the potential for exploring new links among fisheries, fish populations, and other factors influencing the marine ecosystem.

The symposium also dealt with communication of scientific information, both within the scientific community and to external clients. Scientific communication has been greatly facilitated by the expansion in computer networks; for example, the symposium was coordinated via Internet. Future fisheries issues may be decided largely in the public forum, with relevant assessment data disseminated via Internet to competing interest groups (Schnute and Richards 1994). Meanwhile, communication is critically important between fishery scientists and the managers who implement resource decisions; how managers react to the failure of management

actions may determine the risk to the fishery resource (Walters 1994).

The Future of Stock Assessment

What is the future of stock assessment? Schnute and Richards (1994) provide their vision of stock assessment in the twenty-first century. Certainly, new analytical tools will continue to provide opportunities for a deeper understanding of the biological and physical processes underlying fisheries ecosystems. Although these tools will help clarify potential consequences of various management options, forecasting of fisheries populations will remain inherently uncertain. Furthermore, important resource issues cannot be addressed without long time series, incorporating several cycles of natural population fluctuation. Not uncommonly, stock assessment data collected more than a few decades ago are discounted today as unreliable. Thus, our future ability to resolve among competing scenarios depends critically on current data collection, preservation, and documentation.

Fortunately, current researchers bring an overwhelming enthusiasm to the demands of stock assessment. The following collection of papers exemplifies some of their achievements to date in the quantitative analysis of fisheries data. While the collection is not intended to be comprehensive, it does characterize the breadth and sophistication of modern fisheries analysis as practiced in North America. We believe that the methods discussed here are a prelude to new opportunities for addressing the challenges ahead.

Acknowledgements

We would like to thank all who participated in the symposium. The symposium's success was due to the dedication of many talented speakers, authors, and reviewers.

References

ANTHONY, V.C. 1993. The state of groundfish resources off the northeastern United States. Fisheries 18(3): 12–17.

COLLIE, J.S., AND P.D. SPENCER. 1994. Modeling predator–prey dynamics in a fluctuating environment. Can. J. Fish. Aquat. Sci. 51: 2665–2672.

FAO (FOOD AND AGRICULTURAL ORGANIZATION OF THE UNITED NATIONS). 1994. Review of the state of world marine fishery resources. FAO Fish. Tech. Pap. 335: 136 p.

HUTCHINGS, J.A., AND R.A. MYERS. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. 51: 2126–2146.

JACOBSON, L.D., AND A.D. MACCALL. 1995. Stock recruitment models for Pacific sardine (*Sardinops sagax*). Can. J. Fish. Aquat. Sci. 52: (In press)

KLEIBER, P., AND J. HAMPTON. 1994. Modeling effects of FADs and islands on movement of skipjack tuna (Katsuwonus pelamis): estimating parameters from tagging data. Can. J. Fish. Aquat. Sci. 51: 2642–2653.

MCALLISTER, M.K., E.K. PIKITCH, A.E. PUNT, AND R. HILBORN. 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. Can. J. Fish. Aquat. Sci. 51: 2673–2687.

MEGREY, B.A., A.B. HOLLOWED, AND R.T. BALDWIN. 1994. Sensitivity of optimum harvest strategy estimates to alternative definitions of risk. Can. J. Fish. Aquat. Sci. 51: 2695–2704.

NMFS (NATIONAL MARINE FISHERIES SERVICE). 1993. Our living oceans: report on the status of U.S. living marine resources, 1993. NOAA Tech. Mem. NMFS-F/SPO-15, Silver Spring, Md.

QUINN, T. J. II., AND N.J. SZARZI. 1993. Determination of sustained yield in Alaska's recreational fisheries, p. 61–84. *In* G. Kruse, D.M. Eggers, R.J. Marasco, G. Pautzke, and T.J. Quinn II [ed.] Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. Alaska Sea Grant College Program Rep. No. 93-02, University of Alaska Fairbanks, Fairbanks, Alaska.

ROSENBERG, A.A., M.J. FOGARTY, M.P. SISSENWINE, J.R. BEDDINGTON, AND J.G. SHEPHERD. 1993. Achieving sustainable use of renewable resources. Science (Wash., D.C.) 262: 828–829.

ROSENBERG, A.A., AND V.R. RESTREPO. 1994. Uncertainty and risk evaluation in stock assessment advice for U.S. marine fisheries. Can. J. Fish. Aquat. Sci. 51: 2715–2720.

SAMPSON, D.B. 1994. Fishing tactics in a two-species fisheries model: the bioeconomics of bycatch and discarding. Can. J. Fish. Aquat. Sci. 51: 2688–2694.

SCHNUTE, J.T., AND L.J. RICHARDS. 1994. Stock assessment for the 21st century. Fisheries 19(11): 10–16.

SMITH, S.J., J.J. HUNT, AND D. RIVARD. 1993. Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

THOMPSON, G.G. 1994. Confounding of gear selectivity and the natural mortality rate in cases where the former is a nonmonotone function of age. Can. J. Fish. Aquat. Sci. 51: 2654–2664.

WALTERS, C.J. 1994. Use of gaming procedures in evaluation of management experiments. Can. J. Fish. Aquat. Sci. 51: 2705–2714.

Modeling Effects of FADs and Islands on Movement of Skipjack Tuna (*Katsuwonus pelamis*): Estimating Parameters from Tagging Data

P. Kleiber

Southwest Fisheries Science Center, U.S. National Marine Fisheries Service, La Jolla, CA 92038, USA

and J. Hampton

Oceanic Fisheries Programme, South Pacific Commission. Noumea, New Caledonia

Kleiber, P., and J. Hampton. 1994. Modeling effects of FADs and islands on movement of skipjack tuna (*Katsuwonus pelamis*): estimating parameters from tagging data. Can. J. Fish. Aquat. Sci. 51: 2642–2653.

From an experiment with ordinary dart tags, we have found evidence of the effect of fish-aggregating devices (FADs) and of islands on the movements of skipjack tuna (*Katsuwonus pelamis*) around the Solomon Islands. By fitting a fish movement model to the tag data, we were able to estimate mortality and movement parameters (including diffusivity), parameters of a function that models FAD attraction, and a separate parameter of island attraction. Diffusivity was high enough to effectively distribute fish throughout the island archipelago (approximately 150 000 km^2) within a few months. Estimates of FAD parameters indicate that the presence of up to four or five FADs in an area approximately 50 × 50 km can reduce the propensity for skipjack to leave that area by approximately 50%, but that deploying additional FADs in such an area does not significantly increase their effectiveness in holding skipjack. Estimates of the island attraction parameter imply that the propensity of skipjack for movement away from the archipelago is less than half the propensity for movement within it.

Grâce à une expérience de marquage avec des étiquettes-dards ordinaires, nous avons fait la preuve des effets des dispositifs concentrateurs de poissons (DCP) et des îles sur les déplacements des bonites à ventre rayé (*Katsuwonus pelamis*) autour des îles Salomon. En ajustant un modèle du déplacement des poissons avec les données de marquage, nous avons pu estimer les paramètres de la mortalité et du déplacement (y compris la diffusivité), les paramètres d'une fonction qui modèle l'attraction des DCP, et un paramètre différent pour l'attraction des îles. La diffusivité était assez forte pour répartir efficacement les poissons sur l'ensemble de l'archipel (environ 150 000 km^2) en quelques mois. Les estimations des paramètres des DCP indiquent que la présence de quatre ou cinq DCP dans une zone d'environ 50 × 50 km peut réduire de 50 % environ la propension des bonites à quitter cette zone, mais que le mouillage de DCP supplémentaires n'augmente pas de façon notable la capacité de rétention des bonites. Les estimations du paramètre d'attraction des îles indiquent que la propension des bonites à s'éloigner de l'archipel est inférieure à la moitié de leur propension à se déplacer à l'intérieur de l'archipel.

Received July 31, 1994
Accepted October 4, 1994
(J12255)

Reçu le 31 juillet 1994
Accepté le 4 octobre 1994

It is well known that tropical tunas aggregate around floating objects, including artificial fish-aggregating devices (FADs) deployed specifically to improve fishing success by concentrating the tuna (Brock 1985). Tracking studies with acoustic tags have demonstrated effects of FADs on movement behavior of various tropical tuna species (Cayré and Chabanne 1986; Holland et al. 1990; Cayré 1991). These tracking studies deal with individual animals perhaps in the vicinity of one or a few FADs. They typically cover a time scale of days and a spatial scale of tens of kilometres. It is not clear how to extrapolate the findings to longer term movement within a population of tunas in a large area occupied by a given spatial arrangement of many FADs. Using the results of a tagging study with simple dart tags on the time scale of months and spatial scale of hundreds of kilometres (Solomon Islands archipelago), and working with a tuna movement model, we have now detected evidence of the effects of many FADs deployed throughout the archipelago on movement behavior of a population of skipjack tuna (*Katsuwonus pelamis*). We have also detected a separate effect of the islands on skipjack movement.

The tagging study was conducted during 1989–1990 by the South Pacific Commission and the Solomon Islands Ministry of Natural Resources. The Solomon Islands consist of a main group archipelago (MGA) and several outlying islands or atolls (Fig. 1). A local tuna fishery operating there has, in recent years, produced 30 000 – 40 000 metric tons of tuna annually, the majority of which has been skipjack. Two main fishing techniques are employed, pole-and-line and purse seine. The pole-and-line fleet, consisting of 30 Japanese-type vessels, has unrestricted access throughout the Solomon Islands Exclusive Economic Zone outside of three miles from land, but most vessels usually fish within, or just outside, the MGA baseline (Fig. 2), where they are in close proximity to productive baiting grounds. The purse-seine fleet, consisting of one single seiner and three group seiners,

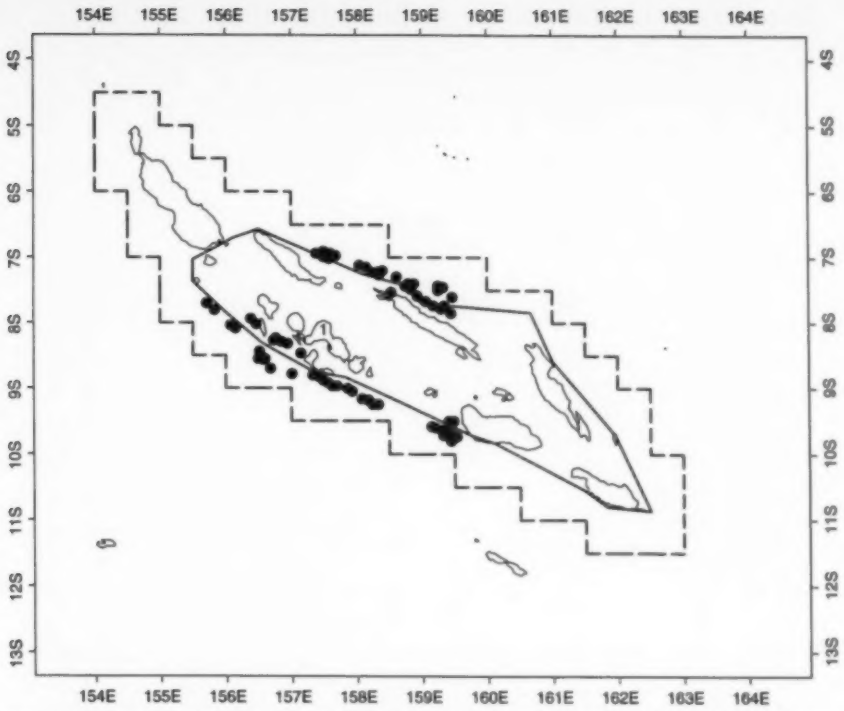


FIG. 1. Study area, showing the Solomon Islands main group archipelago (MGA) baseline (heavy line), the locations of FADs (large dots), and the "archipelagic fence" (broken line). 1 = New Georgia Island.

is excluded from waters within the MGA baseline, and bases its operations around setting on FADs moored just outside that line (Fig. 3). Pole-and-line vessels may also fish near these FADs and near others that are moored inside the MGA baseline, but their operations are much less FAD dependent than those of the purse seiners.

The principal objective of the tagging study was to quantify deleterious effects, if any, that the two fleets might have on each other, and to help set fishery development targets and strategies. Preliminary analysis of the tag data showed that the purse-seine tag return rate relative to that of the pole-and-line fleet was substantially higher than expected based on the relative catch of untagged skipjack by the two fleets. It was surmized that the locations of tag releases in relation to the locations of the FADs was a key determinant in the pattern of tag recoveries by gear type (SPC 1990). To carry the analysis further, we developed a population dynamics model to describe skipjack natural death, harvest, and movement. In its final form, the model explicitly incorporates the effects of FADs and islands on skipjack movement. We were able to fit the model to the tagging data and thereby estimate parameters of skipjack association with FADs and with islands.

Tagging Operations

Tagging in the Solomon Islands was conducted as part of a wider scale tagging effort, the Regional Tuna Tagging Project, a full description of which is given in SPC (1988). In the Solomon Islands, the experimental design called for tagged skipjack, of the size range normally found in commercial catches (40–60 cm fork length), to be released throughout the major area of operation of the fishery. In particular, tagged skipjack were to be released both in areas fished by purse seiners (in the vicinity of FADs) and in areas fished by pole-and-liners (mainly within the MGA baseline). Four cruises were undertaken on pole-and-line vessels that were fishing commercially (in July–August 1989, October–November 1989, March 1990, and June 1990). Therefore, most releases were made to the south of New Georgia Island, which was the most productive fishing ground during these cruises (Fig. 4). Three additional cruises were undertaken in December 1989 – January 1990, February–March 1990, and September–October 1991, using a chartered research vessel, to release tagged skipjack in as many spatial strata as possible. In all, 11 892 skipjack were tagged, from which 1654 returns have been recorded. (In addition, 2725 yellowfin tuna (*Thunnus albacares*) were released resulting in 237 returns.) The work described here is confined to the skipjack data pertaining to tagging cruises in 1989 and 1990: 7730 releases and 914 returns. Of these returns, 115 were excluded because they were caught by other than the two Solomon Islands commercial fleets or because they were not accompanied by sufficient information to determine the time–area stratum of recovery. Returns from other fleets were excluded because of lack of complete fishery data. Thirty of the excluded returns were caught outside the study area. Data from the September–October 1991 cruise were excluded because substantial numbers of returns were still being received as this analysis was taking place.

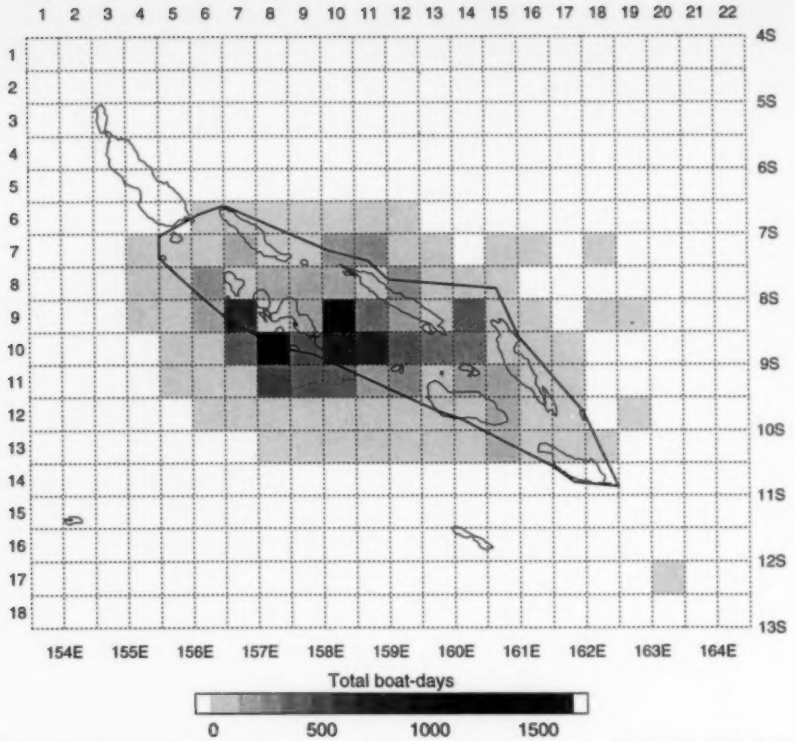


FIG. 2. Aggregate distribution of pole-and-line effort in the study area from mid-1989 through 1991.

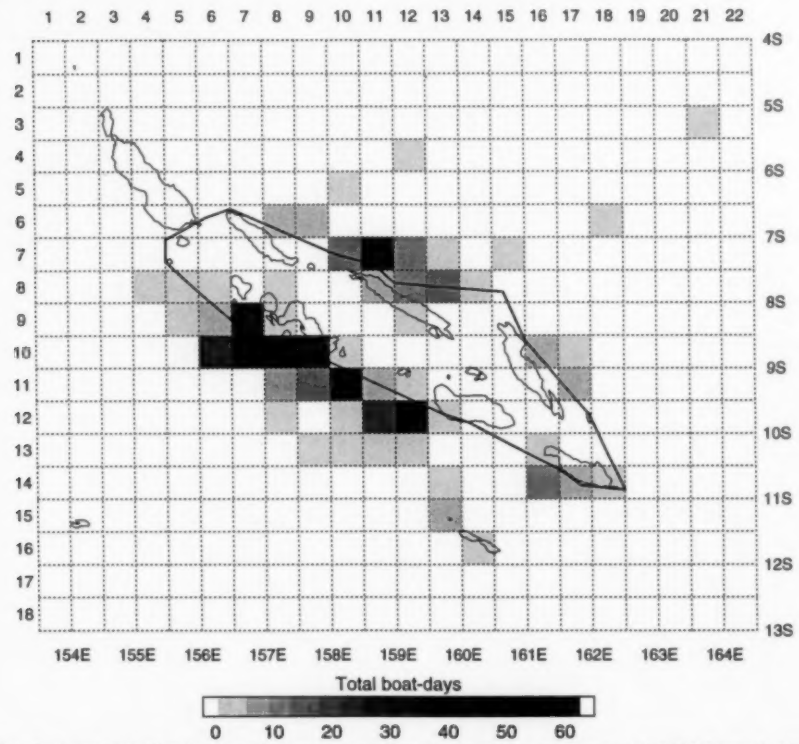


FIG. 3. Aggregate distribution of purse-seine effort in the study area from mid-1989 through 1991.

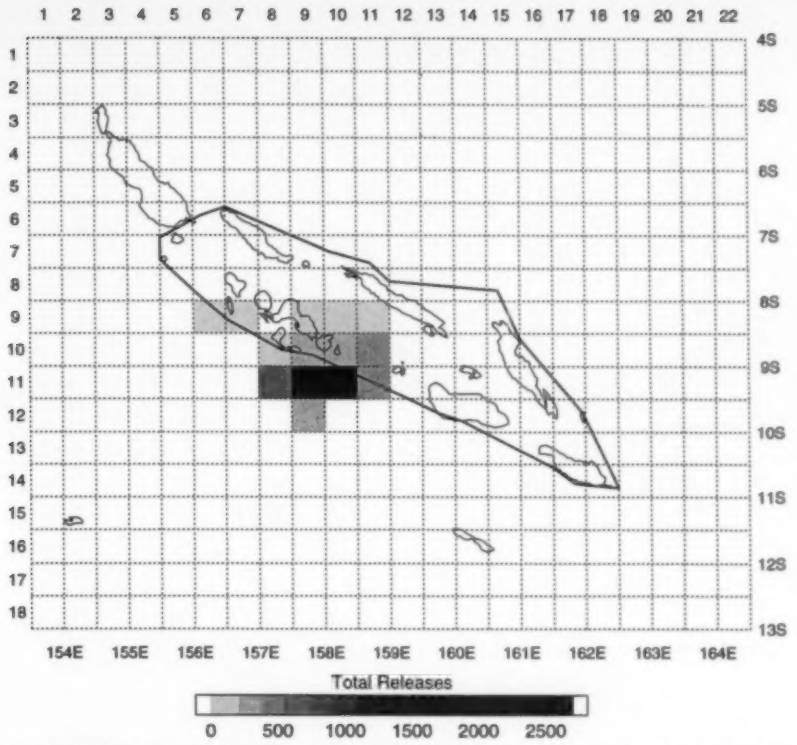


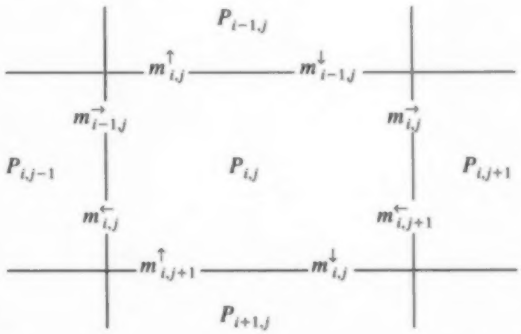
FIG. 4. Distribution of skipjack tag releases from tagging cruises in the Solomon Islands, 1989–1990.

Tagged Fish Dynamics Model

The model deals with three basic processes: natural death, harvest, and movement in two horizontal dimensions. The model does not need to deal with growth or age because we assume that during their short lifetime of exposure to the fishery, skipjack do not change their characteristics of mortality, vulnerability to the fishery, or movement. Tag data indicate that the average exposure of skipjack to a fishery is less than 1 yr (Kleiber et al. 1987; SPC 1990). Recruitment in the model is driven by the release of tagged fish at known times and places. (Henceforth in this paper, tagged fish will be referred to as tags.)

Most of the complexity of the model resides in the way it deals with movement. It is an advection–diffusion model on a discrete spatial grid of half-degree squares. Thus the grid spacing is approximately 50 km (30 nautical miles) in both spatial dimensions. The geographic boundaries (any of Figs. 1–4) are such that we have an 18×22 spatial grid, and the population of tagged fish at large at any time, t, is represented by an 18×22 matrix, $\mathbf{P}_t$. Time is discretized into 1-mo intervals. The spacing of time and spatial intervals reflects the resolution of the available data, both for tag recovery times and positions and for distribution of fishing effort — both necessary inputs to the model.

Movement in the model is regulated by transfer coefficients, two of which are assigned to each grid cell boundary — one in each direction. This means that there are four matrices of transfer coefficients, $\mathbf{m}^{\uparrow}$, $\mathbf{m}^{\downarrow}$, $\mathbf{m}^{\rightarrow}$, $\mathbf{m}^{\leftarrow}$, which govern movement in the north, south, east, and west directions, respectively. The relationship of elements of the population matrix and the movement coefficient matrices to grid cells is organized as follows:



The movement coefficients are the proportion of the fish in one cell that move to a neighboring cell per unit time. For example, the instantaneous rate of movement from cell (i,j) to $(i,j+1)$ would be given by $m^{\rightarrow}_{i,j}P_{i,j}$.

Adding up the effects of movement, mortality, and tag release, the difference equation for projecting the population of tagged fish in cell (i,j) at time t by one time step, Δt, is given by

$$(1)\quad P_{i,j,s+\Delta t} = P_{i,j,s} + R_{i,j,s} + \Delta t\Big[m^{\uparrow}_{i+1,j}P_{i+1,j,\tau} + m^{\downarrow}_{i-1,j}P_{i-1,j,\tau} + m^{\rightarrow}_{i,j-1}P_{i,j-1,\tau} + m^{\leftarrow}_{i,j+1}P_{i,j+1,\tau} - \Big(m^{\uparrow}_{i,j} + m^{\downarrow}_{i,j} + m^{\rightarrow}_{i,j} + m^{\leftarrow}_{i,j} + M\Big)P_{i,j,\tau} - \sum_{g}\hat{r}_{i,j,g,s}\Big]$$

where τ is either t or $t + \Delta t$, $R_{i,j,s}$ is the number of tags released in cell (i,j) at time t, and M is the natural mortality and where

$$\hat{r}_{i,j,g,s} = q_g e_{i,j,g,s} P_{i,j,\tau}$$

is the catch of tagged fish by gear g in the cell (i,j) during the time interval t to $t + \Delta t$, with q_g the catchability for the gth gear type and $e_{i,j,k,t}$ the corresponding effort (vessel-days) of gear k in the time interval. The two gear types in the present implementation of the model, purse seine and pole-and-line, account for almost all (>99%) of the tag returns.

Choosing τ to be t or $t + \Delta t$, determines whether explicit (t) or implicit ($t + \Delta t$) time stepping is used to generate a solution to the above difference equation. We used an alternating direction, implicit method (Press et al. 1988, pp. 666), similar to the method developed by Sibert and Fournier (1993) for a large-scale tuna movement model. With four subiterations per time step, we were able to get stable solutions with large movement turnover of several hundred percent per time step in the grid cells.

Equation 1 deals with movement in terms of transfer coefficients. It is a temporally and spatially discretized form of a continuous, partial differential equation model in which movement is governed by diffusion and advection parameters. The relation between diffusion and advection in the continuous model and transfer coefficients in the discrete model is outlined in Appendix A.

Determining Movement Coefficients

In the absence of local conditions that would affect movement behavior, all transfer coefficients in the model would be assigned a common value D. We will refer to this parameter as the diffusivity because without further modification of the transfer coefficients, movement would be purely diffusive. However, the presence of FADs or islands does modify the values that are assigned to local transfer coefficients as follows:

$$(2)\quad \begin{aligned} m^{\uparrow}_{i,j} &= D\cdot\phi_{i,j}b^{\uparrow}_{i,j}/a_{i,j} \\ m^{\downarrow}_{i,j} &= D\cdot\phi_{i,j}b^{\downarrow}_{i,j}/a_{i,j} \\ m^{\rightarrow}_{i,j} &= D\cdot\phi_{i,j}b^{\rightarrow}_{i,j}/a_{i,j} \\ m^{\leftarrow}_{i,j} &= D\cdot\phi_{i,j}b^{\leftarrow}_{i,j}/a_{i,j} \end{aligned}$$

where $\phi_{i,j}$ is an element of matrix $\mathbf{\Phi}$, describing effects of FADs, and $b^{\uparrow}_{i,j}$, $b^{\downarrow}_{i,j}$, $b^{\rightarrow}_{i,j}$, $b^{\leftarrow}_{i,j}$, and $a_{i,j}$ are elements of corresponding matrices $\mathbf{b}^{\uparrow}$, $\mathbf{b}^{\downarrow}$, $\mathbf{b}^{\rightarrow}$, $\mathbf{b}^{\leftarrow}$, and $\mathbf{a}$, describing various effects of islands.

FAD effect

Other than the well-known and well-utilized observation that tunas congregate in the neighborhood of FADs, little is known about how FADs might modify movement behavior. Observations of course tracks of individual tunas (Cayré and Chabanne 1986; Holland et al. 1990) in some cases show obvious attraction to FADs, but it is not obvious how to translate these observations into numerical parameters of movement. In our model, we have assumed that FADs in a grid cell inhibit the movement of fish out of that cell. This is accomplished by reducing the exit coefficients of cells by factors which are the corresponding elements of $\mathbf{\Phi}$, given by

$$(3)\quad \phi_{i,j} = s + (1-s)e^{-\frac{\ln(2)}{f_h}f_{i,j}};\qquad 0 \le s \le 1, f_h \ge 0$$

where $f_{i,j}$ is the number of FADs in cell (i,j). This formula is designed such that cells with no FADS have no effect ($\phi = 1$), and such that with increasing numbers of FADs, the effect increases (ϕ decreases) and approaches a saturation level ($\phi \to s$) for cells with a large number of FADs. The parameter f_h is the number of FADs in a cell that gives half the saturation effect. A theoretical justification for Equation 3 is given in Appendix B.

Island effects

Islands modify transfer coefficients both by obstructing the water area within cells and by altering the permeability of boundaries between cells. Permeability is reduced either by direct obstruction of the boundaries or by what we call the "archipelagic fence" (Fig. 1 and see below).

The elements of the four **b**-matrices $\mathbf{b}^{\uparrow}$, $\mathbf{b}^{\downarrow}$, $\mathbf{b}^{\rightarrow}$, $\mathbf{b}^{\leftarrow}$, govern the permeability of cell boundaries, as shown in Equations 2. If a cell boundary is unobstructed by islands, and it does not lie along the archipelagic fence, then the corresponding elements of the appropriate pair of these matrices (the north–south pair or the east–west pair) will both be set to 1. However, if the boundary is obstructed, both corresponding **b**-matrix elements are set to the proportion of the boundary that is not obstructed. We estimated the proportions from a slightly altered Solomon Islands map on which we shifted some of the islands slightly to prevent the situation of cells being cut into two isolated parts, the data resolution being insufficient to assign effort and tag returns to subareas within cells. In these cases, we guessed which side of the island most of the data originated from and shifted the island so that all the water area in the cell was on that side.

As described below, we found an apparent reluctance for fish to leave the vicinity of the archipelago, but we could not model this effect with the simple expedient of reducing the diffusivity in the neighborhood of the islands because there also appears to be high mobility within the archipelago. We therefore imagined that there is a peculiar kind of fence surrounding the archipelago and located along cell boundaries (Fig. 1). The fence allows free movement in the inward direction but restricted movement in the outward direction. The degree of restriction is measured by a parameter F_f, between 0 and 1 — the "fence factor". For each of the cell boundaries along the fence, we reduced the corresponding element of the **b**-matrix governing the direction across the particular boundary going out of the archipelago by multiplying by F_f. Thus, a value of 0 for F_f implies no leakage, and a value of 1 implies complete permeability.

To deal with obstruction of water area within cells, we estimated for each cell the proportion of the area that is open (i.e., *not* obscured by islands). We entered these proportions into the corresponding elements of matrix **a**.

The obscuring of area in cells by islands has an additional effect, not on movement, but on fishing mortality.

A given amount of effort is more effective if the fish and the gear are crowded into a smaller area. In the model, we handled this by enhancing the effort by the reciprocal of the area factor, that is,

$$(4) \quad e_{i,j,g,t} = e^{o}_{i,j,g,t} / a_{i,j} \; \forall \; i, j, g, t$$

where $e^{o}_{i,j,k,t}$ is the observed effort.

Edges of model grid

The edges of the grid must be handled specially. In this model, we have closed borders, which means that no fish can migrate into or out of our model area. In effect, the transfer coefficients of the outer boundary are defined to be 0, that is, for our 18 × 22 grid:

$$(5) \quad \begin{aligned} &m^{\uparrow}_{1,j}, m^{\downarrow}_{0,j}, m^{\uparrow}_{19,j}, m^{\downarrow}_{18,j} \equiv 0 \; \forall \; j \\ &m^{\leftarrow}_{i,1}, m^{\rightarrow}_{i,0}, m^{\leftarrow}_{i,23}, m^{\rightarrow}_{i,22} \equiv 0 \; \forall \; i. \end{aligned}$$

However, we effectively opened the borders by setting the edge elements of the surface area matrix **a** to values much greater than unity (normally these numbers are proportions, i.e., between 0 and 1). This had the effect of making the edge cells into population sinks because their surface areas were, in effect, much larger than the interior cells.

Fitting Model to Tag Data

We used a strategy similar to that of Hilborn (1990), Deriso et al. (1991), and Sibert and Fournier (1993) to fit the model to tag data. In our case, we maximized a likelihood function which is the probability of observing what we did observe (the real data), under the assumption that the returns predicted from the model are the expected values for the returns. We used a different likelihood function for each of two different simulation modes.

Simulation Modes

In one simulation mode, we modeled the fate of all members of a set of tags released within a calendar month and within one half-degree square. There were 27 such sets in the tagging programme (Table 1), and a separate run of the model was required for each set that we considered. A run, in this case, consisted of generating a solution to Equation 1 from the month of release through the month of the last tag return or beyond. The population of tagged fish started at zero everywhere except for the release square which started with the effective number released (see below) in the tag set. There are no other recruitment events in this simulation mode.

In the second simulation mode, we considered all the tag data in aggregate with simulation starting at month 1 and proceeding through month 28 (the last month for which we had complete effort data). In this case, we had multiple recruitment events with Table 1 giving the schedule of times, locations, and total numbers released which were multiplied by the initial tag survival factor to get effective recruitment. Once tagged fish are recruited, they are indistinguishable from other tagged fish that happen to be in the same half-degree square. Therefore, in this mode the model cannot associate predicted recoveries with particular release sets.

Likelihood Functions

In the first simulation mode in which a single release set is modeled at a time, the probability of any one tag being returned from a particular time–area–gear stratum is given by the model as

TABLE 1. Monthly and half-degree square release sets ordered by number of releases. Months are numbered from 1, beginning in July 1989. Rows and columns are the latitude and longitude indices, respectively, for half-degree squares corresponding to the scheme in Fig. 1. Total returns includes only the number of returns with enough information to determine the month and half-degree square of recovery. Final month is the month in which the last such recovery was made.

	Releases				Total	Final
Set	Month	Row	Column	Number	returns	month
1	2	11	9	1938	237	27
2	12	11	10	1817	82	25
3	2	11	8	637	41	10
4	9	11	10	473	142	17
5	1	11	11	444	76	16
6	2	11	10	328	55	14
7	9	10	9	314	6	17
8	12	10	11	248	14	17
9	12	10	10	206	9	25
10	1	10	11	182	27	14
11	9	11	8	162	17	15
12	2	9	7	136	61	12
13	9	11	9	131	10	14
14	2	12	9	120	17	21
15	9	12	9	92	4	14
16	1	11	10	64	10	5
17	9	10	10	63	16	10
18	5	9	6	62	0	—
19	1	9	11	58	9	6
20	1	10	10	54	9	14
21	1	9	10	51	4	4
22	5	9	7	49	2	12
23	12	10	8	45	0	—
24	12	11	11	27	2	16
25	1	9	9	23	7	12
26	9	9	7	5	0	—
27	9	10	8	1	0	—

$$(6) \quad p_{i,k} = \frac{\hat{r}_{i,k}}{R_k}$$

where $\hat{r}_{i,k}$ is the predicted number of tag returns in stratum i and tag set k (index i covers time, area, and gear dimensions) and R_k is the effective number of releases in tag set k.

The probability of not being returned for a tag in set k, then, is $1 - \sum_i p_{i,k}$. Combining the probabilities of all the actual tag returns as well as the probabilities for all the tags that were not returned, the likelihood of the observed data, $\mathbf{r}$, given the predicted data $\hat{\mathbf{r}}$, is the following product of multinomial functions

$$(7) \quad \mathcal{L}_1(\mathbf{r} \mid \hat{\mathbf{r}}) = \prod_k \left[\frac{R_k!}{(\prod_i r_{i,k}!)(R_k - \sum_i r_{i,k})!} \left(1 - \frac{\sum_i \hat{r}_{i,k}}{R_k}\right)^{(R_k - \sum_i r_{i,k})} \prod_i \left(\frac{\hat{r}_{i,k}}{R_k}\right)^{r_{i,k}} \right]$$

where $r_{i,k}$ is the observed number of tag returns in stratum i and tag set k. Note that this scheme can deal with more than one tag set, but the sets are only combined after the predicted returns for each set are determined in separate simulation runs, which means that computation time can be

TABLE 2. Results of fitting model, giving the salient conditions of each fit, the parameter values to which the procedure converged, and the negative log likelihood measure of goodness-of-fit. Numbers in the tag set column refer to the set numbers in Table 1 and indicate that the first simulation mode (individual tag sets) is used in the fit whereas "agg" in this column indicates that all the tag data are entered into the fit using the second simulation mode (multiple recruitment events and aggregated tag data). Parameters and their units are diffusivity (D, cell-area·mo^{-1}), saturation FAD effect (s, unitless), half-saturation number of FADs (f_h, no. of FADs), fence factor (F_f, unitless), natural mortality (M, mo^{-1}), and catchability (q, cell-area·boat-day^{-1}·mo^{-1}).

	Conditions			Estimated parameters							
Fit	FAD	Fence	Tag sets	D	s	f_h	F_f	M	Purse-seine q	Pole-and-line q	Goodness-of-fit $-\log(\mathcal{L})$
1	+	+	1	3.1	0.25	1.3	0.72	0.17	0.028	0.0012	347.62
2	+	+	2	2.3	0.90	0.3	0.69	0.07	0.011	0.00033	195.07
3	+	+	3	2.2	0.15	1.7	1.0	0.23	0.016	0.00078	108.27
4	−	−	1, 2	2.7	—	—	—	0.11	0.037	0.00089	604.49
5	+	−	1, 2	3.2	0.41	1.3	—	0.12	0.023	0.00078	595.51
6	−	+	1, 2	2.6	—	—	0.28	0.15	0.027	0.00064	598.16
7	+	+	1, 2	3.2	0.49	1.3	0.36	0.15	0.020	0.00064	590.92
8	−	−	agg	2.0	—	—	—	0.19	0.053	0.0013	1229.8
9	+	−	agg	2.5	0.55	1.7	—	0.19	0.042	0.0013	1218.2
10	−	+	agg	2.1	—	—	0.44	0.22	0.045	0.0011	1224.1
11	+	+	agg	2.6	0.59	1.8	0.55	0.22	0.039	0.0012	1215.6

prohibitive if more than a few tag sets are combined in one optimization run.

To deal with all 27 tag release sets in one optimization, we used the second simulation mode which allows reasonable computation time but has the disadvantage that the multinomial distribution cannot be applied because the predicted tag recoveries are no longer associated with particular release sets. In this case, we assume that the probability of a given number of tag returns is given by the Poisson distribution, where the mean of the distribution for a particular time–area stratum is the number of returns for that stratum predicted by the model. Thus, we have

$$(8) \qquad \mathcal{L}_2(\mathbf{r} \mid \hat{\mathbf{r}}) = \prod_i \frac{\hat{r}_i^{r_i}}{e^{\hat{r}_i} r_i!}$$

where

$$r_i = \sum_k r_{i,k}$$

is the observed number of tag returns in a stratum i and $\hat{r}_i$ is the predicted number of tag returns in stratum i. Note that in this case, the observed tag returns are aggregated over tag sets before entering into the likelihood formula, and the predicted tag returns are automatically aggregated in this way in the model.

In both modes the likelihood function depends on the predicted returns which depend, in turn, on the parameter values in the model. Thus, we can fit the model and estimate parameters by searching for the set of parameter values that maximizes the likelihood function. Actually, we searched for the minimum of the negative log of the likelihood function, making use of the programming package AUTODIF, which is designed for nonlinear function minimization using an iterative quasi-Newton routine and a built-in system for automatically finding the required partial derivatives of the function being minimized (Otter Research 1991). In estimating up to seven parameters consisting of diffusivity, two FAD parameters, the archipelagic fence factor, natural mortality, and two catchabilities, the fitting procedure tends to converge in 10–100 iterations, depending on how close the original parameter guesses are to the final estimates.

Effective Releases

The effective number of releases is the total number released multiplied by an initial tag survival factor, $\alpha\beta$. This factor is not precisely known. It includes α, the proportion of tags that survive immediate tag shedding and immediate tagging mortality, and β, the reporting rate, that is, the proportion of recaptured tags that are reported with satisfactory recovery information. Tagging mortality and shedding have been estimated to be minor effects in this and earlier skipjack tagging campaigns (Kleiber et al. 1987; Hampton 1992). Therefore, α should be not much less than 1. For the tagging campaign under analysis here, the reporting rate for the two Solomon Islands fleets should have been close to 1 due to exceptionally vigorous publicity efforts and substantial tag return awards. This was confirmed by 100% return of five tagged fish clandestinely seeded in the catch.

To investigate sensitivity of parameter estimates to $\alpha\beta$, we compared fits to tag set 1 with $\alpha\beta$ set to 1.0 and 0.67. The catchability estimates increased approximately 50% with the reduction in $\alpha\beta$, but other parameters were much less affected: 7% change for natural mortality and less than 3% change for the various parameters involved in movement. All other fits reported here were conducted assuming a relatively high value of 0.9 for $\alpha\beta$.

Results

Fitting the model in the first mode was attempted on the top 12 tag sets, ranked by number of releases, in Table 1. Convergence was readily achieved for tag sets with large numbers of releases. Fits on five of the tag sets with less than 400 releases did not converge on the first attempt. Three of these fits failed because of unstable simulations that predicted negative populations, and one of these was

TABLE 3. Parameter correlation matrix from model Fit 7.

	D	s	f_h	F_f	M	q_s	q_p
D	1.00						
s	−0.24	1.00					
f_h	−0.31	−0.44	1.00				
F_f	−0.19	−0.19	−0.03	1.00			
M	0.04	0.02	0.06	−0.58	1.00		
q_s	0.00	0.33	0.04	0.39	−0.02	1.00	
q_p	0.21	−0.10	−0.05	0.50	−0.05	0.48	1.00

induced to converge by increasing the number of subiterations. Fits conducted in the second mode, with all the tag data combined, converged readily.

Results from the three largest sets are given in Table 2, along with results from a combination of sets 1 and 2, plus results from fitting in second mode to all the data. All fits shown in Table 2, when repeated with different starting values for the parameters, reconverged to essentially the same points.

Fits 4–7 are combined fits to the two tag sets with the greatest numbers of releases (49% of all releases in the tagging programme). These fits comprise all combinations of enabling or disabling either the FAD effect or the archipelagic fence effect. The parameter estimates are more stable than with fits to individual tag sets (Fits 1–3). Adding the FAD effect, the archipelagic fence effect, or both improved the goodness of fit. An approximate test of significance shows that all differences in Fits 4–7 are significant with probability values less than 10^{-3}. The test is based on a χ^2 value of twice the difference in log-likelihood with degrees of freedom equal to the difference in number of parameters

Fits 8–11 are similar to Fits 4–7, but with the model in the second (aggregate data) mode. The results are similar to Fits 4–7. The parameter estimates are stable but at somewhat different values, and the χ^2 tests give the same significant results for enabling the FAD effect or the archipelagic fence effect.

The parameter correlation matrix calculated from the inverse Hessian matrix (Press et al. 1988, pp. 544) is given in Table 3 for Fit 7. The strongest correlation is a negative one between the natural mortality estimate and the fence factor. The catchabilities of both fleets show some positive correlation with the archipelagic fence factor and with each other.

Discussion

To evaluate graphically the performance of the model by comparing real and predicted tag returns is difficult because of the multidimensional nature of the data (tag set, gear type, month, latitude, longitude). However, comparisons of various aggregates of the predicted and observed data can be done. In Fig. 5 are shown the overall tag return rates with time-at-large. Confidence bands were obtained by generating 200 artificial data sets (number of tag returns by gear, month, and location) using the multinomial probabilities given by Equation 6 with the final (best fitting) predicted returns $\hat{\mathbf{r}}$ from Fit 7 in Table 2. From these artificial data sets, 200 aggregate tag returns in each months-at-large category were calculated. The 2.5 and 97.5% quantiles from each months-at-large category form the confidence bands

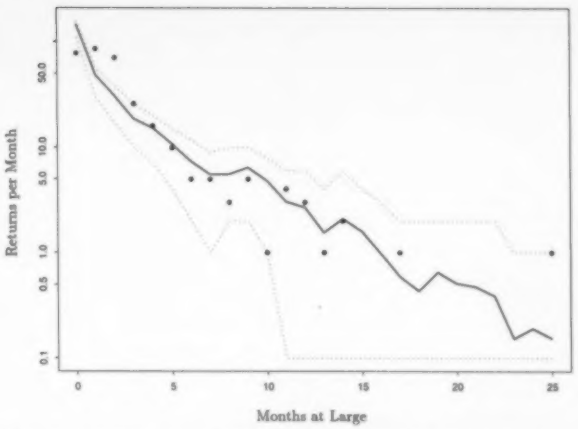


FIG. 5. Aggregate tag attrition. The solid line is expected aggregate returns per month predicted by model Fit 7. Points are the observed aggregate returns for the two tag sets used in fitting the model. The dotted lines are 95% Monte–Carlo confidence bands. The lowest levels of the lower confidence bands are actually zero.

in Fig. 5. If we imagine that the confidence bands were not there, it would appear that the model fit is best in the early months and deteriorates after about 10 mo at large. There is a natural tendency for this to be so in this type of logarithmic attrition plot. The model can legitimately predict fractional returns (even less than one return), but fractional returns cannot happen in reality, nor can zero returns be represented on the logarithmic plot. The effect is that the points tend to be far from the predicted line. This effect is accounted for in the confidence bands, which broaden with time at large, and we can see that the worst fit of the model, according to Fig. 5, is actually in the first 3 mo.

Figure 6 is the mean distance from cell of release with time. The mean distance levels off within 4 or 5 mo, implying that the fish movement is rapid enough to distribute the tagged fish throughout the region of significant fishing effort within that amount of time. The confidence bands were obtained from the 200 artificial data sets similarly to the confidence bands in Fig. 5. Because of diminishing number of predicted tag returns, the confidence bands broaden with time-at-large as in Fig. 5. The worst fit in this case is in the first month where the actual mean distance of recovery was greater than predicted.

Estimation of the FAD parameters s and f_h is the central thrust of this work. Our basic question was whether the model would be sensitive to those parameters. The model fits the data better with the FAD parameters enabled both in individual tag set mode and in aggregate tag mode. Approximate χ^2 tests indicate that the improvement in fit is significant. However, the validity of this test might be affected by violation of the assumption underlying the likelihood function that the tags are independent of each other. If this were true, and if the parameter values used to generate the 200 Monte-Carlo data set were also the true parameter values in nature, and if the processes in the model were in fact the true processes at work in nature, then the real observed tag data are, in fact, a multinomial realization of those processes and parameter values. Given those conditions, any of the 200 artificial data sets would have been

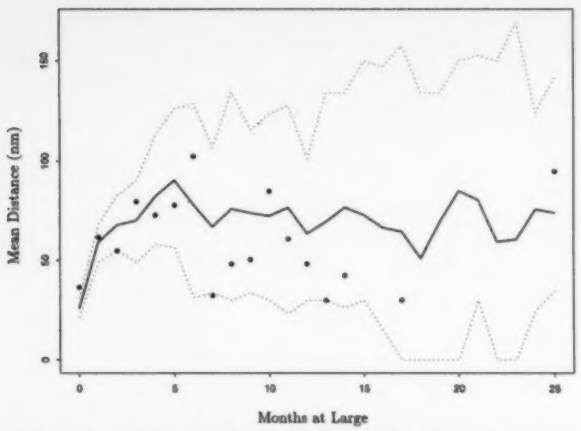


FIG. 6. Mean distance with time. The solid line is mean distance of recoveries from the release point predicted by model Fit 7. Points are the observed mean distance of recoveries for the two tags sets used in fitting the model. The dotted lines are 95% Monte–Carlo confidence bands.

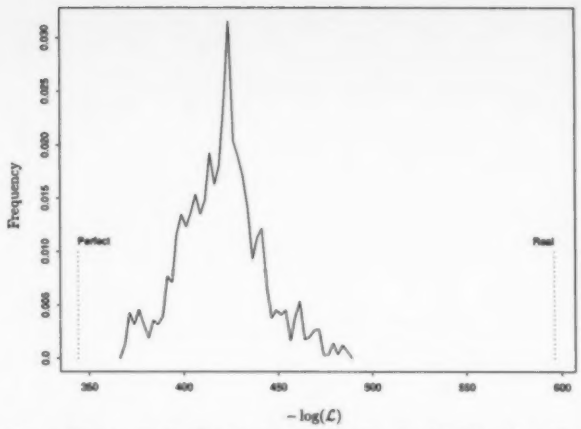


FIG. 7. Monte–Carlo distribution of negative log likelihoods with parameters from model Fit 7. The level marked "perfect" is the negative log likelihood for a hypothetical, and impossible, data set identical to the best fitting outcome of the model — impossible because it contains fractional returns. The level marked "real" is the negative log likelihood for the real tag return data.

an equally likely happenstance as the real data set, which means that the goodness-of-fit of the given parameter values calculated on the basis of any of the artificial data sets would be an equally likely outcome as the goodness-of-fit for those parameter values based on the real data. However, the best (lowest) goodness-of-fit from the real data is in the extreme upper tail of the goodness-of-fit from the artificial data sets (Fig. 7). The poor fit can be attributed to various factors having to do with differences between processes at work in nature and processes at work in the model.

One factor is that the movements of the fish might be more advective than diffusive. The process of advection is not explicitly built into the model, although there is implicit advection resulting from spatial variations due to FADs and islands applied to the transfer coefficients. There is, however, no provision in the model for a broader pattern of advective movement which could easily occur in nature as fish respond to environmental conditions, such as oceanographic gradients. Incorporating this kind of advective movement in the model has not been attempted. In any event, the chief interest of doing so would be in relation to suitably detailed data on environmental conditions extant in the Solomon Islands during the experiment — information that probably does not exist.

Another possible factor is that FADs might affect the catchability within cells as well as, or instead of, the movement between cells. This could be the case if in addition to inhibiting movement out of cells, the FADs channel movement within cells such that the fish are more concentrated and easier to find than they would be without the FADs. Addition of a catchability effect is planned for the next version of the model.

The assumption of tag independence implicit in our likelihood functions is a simplification in the model that does not match the real statistical situation. Because the fish travel in schools, they are not fully independent of each other in their movements. Bayliff (1988) gave evidence that skipjack schools mix with each other such that the average persistence time of fish in a school is on the order of one to several months. Thus, it would seem that the early part of a tagging experiment would track schools rather than fish, but with time the emphasis would shift toward individual fish. From the standpoint of movement processes, we might expect that the model would be indifferent to whether the moving entities are schools or individual fish. However, because there are many fewer schools than fish, we are, in effect, sampling fewer entities than we would suppose if tagged fish were independent of each other. As a result, we would expect that the variability of real results would be greater than implied by our assumption of independence which would lead to larger deviances from the model than anticipated, particularly in the early part of the experiment. This is consistent with what we observed (Fig. 5 and 6). The greater variability would also lead to a worse goodness-of-fit than anticipated, which is again consistent with observation (Fig. 7).

The above factors, as well as others, such as temporal variation in parameters, could lead to extra high stochastic errors and to process errors in the model. Whether they cause bias in parameter estimates is unclear. The effect on our χ^2 tests is also unclear, but there is additional evidence that the FAD effect sensed by the model fits is not just a stochastic coincidence. The FAD attraction submodel (Equation 4) can have a reverse effect, i.e., repulsion, if the parameter s is greater than 1. The fits were conducted with no upper constraint on s. Eight of the fits to individual tag sets successfully converged, and of these, six implied FAD attraction and two implied repulsion. The fits to individual tag sets are independent of each other. Neglecting the magnitudes of the estimates of s, we could view the fits as binomial trials with two possible outcomes: $s < 1$ (FAD attraction) or $s > 1$ (FAD repulsion). Under a null hypothesis of no FAD effect (0.5 probability of either outcome), six out of eight votes for attraction gives a significance probability level of 0.14 in favor of a real FAD attraction — not a spectacular confirmation. However, if we weight the trials by the number of tag returns in the sets, we have 556 votes for attraction out of a possible 659, and the probability level is 2×10^{-76}. From the discussion above, it could be argued

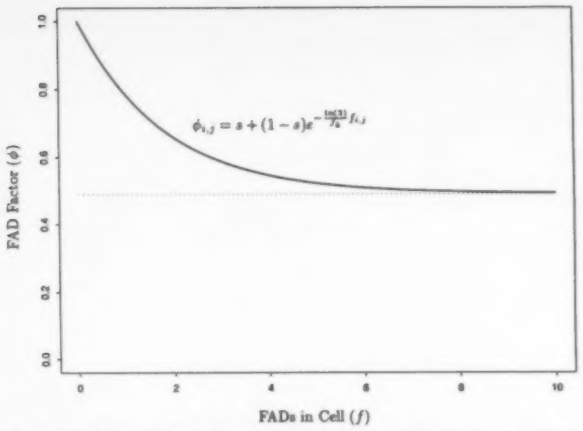


FIG. 8. FAD effect as function of number of FADs in a cell for FAD parameters from model Fit 7. The dotted line is the saturation effect of FADs.

that the appropriate weighting would be the effective number of schools, an ill-defined and unknown quantity. The implication is that the probability level is somewhere between 2×10^{-76} and 0.14.

Additional confirmation of the FAD effect comes from implications of the FAD parameter estimates. They are roughly in line with experience with FADs in Solomon Islands and elsewhere. Taking the values from Fit 11 (Table 2) as the most representative (because all the tag data went into the fit), the tendency of skipjack to exit a cell can be reduced by approximately 50% with four or five FADs in the cell, but the effect of adding more FADs than that is greatly diminished (Fig. 8). Those who have deployed FADs in the Solomon Islands are apparently aware of this limitation. Only a few of the cells are populated with more than five FADs. A radius of FAD action can be calculated from our estimates of f_h (Appendix C). Using f_h from Fit 11, the radius of action is 9 km (assuming FADs placed in a linear array across cells) or 18 km (assuming FADs placed throughout the cells). This range roughly agrees with estimates from tracking studies: "several miles" (Cayré and Chabanne 1986) and "minimum of 5 nmi" (Holland et al. 1990).

Conclusion

We have observed what we think are real FAD effects in classical tag data using a fish movement model. The observations emerged through considerable statistical noise, which may mean that our results are near the fine-scale limit of spatial resolution attainable from such tag experiments. With a mechanistic movement model, we have at least roughly quantified the FAD effect, and it is consistent with other observations, acoustic tracking results in particular. As a result of this, we have connected small-scale tracking of individual fish near individual FADs with movement behavior of a tuna population in a larger scale region sprinkled with FADs. FADs are certainly not the only feature of the environment that could affect tuna movement. It is hoped that similar studies might allow other important environmental features to be incorporated in models that can predict large-scale tuna movements.

Acknowledgements

This work was conducted as part of a collaborative agreement between the United States National Marine Fisheries Service and the South Pacific Commission (SPC) which enabled an extended visit by one of the authors (P. Kleiber) to SPC headquarters in Noumea, New Caledonia. We particularly wish to acknowledge Tony Lewis of the SPC Oceanic Fisheries Programme for organizing many details of that visit including funding from the Australian International Development Assistance Bureau and the European Community. We also want to thank David Fournier and John Sibert for providing AUTODIF software and assisting in its use. And for valuable suggestions on improving this paper, we want to thank John Sibert, Bill Bayliff, Ashley Mullen, Norman Bartoo, Gary Sakagawa, David Simpson, and Patrick Sullivan.

References

ARFKEN, G. 1970. Mathematical methods for physicists. Academic Press, N.Y. 815 p.

BAYLIFF, W.H. 1988. Integrity of schools of skipjack tuna, *Katsuwonus pelamis*, in the eastern Pacific Ocean, as determined from tagging data. Fish. Bull. (U.S.) 86: 631–643.

BROCK, R.E. 1985. Preliminary study of the feeding habits of pelagic fish around Hawaiian fish aggregation devices or can fish aggregation devices enhance local fisheries productivity? Bull. Mar. Sci. 37: 40–49.

CAYRÉ, P. 1991. Behaviour of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) around fish aggregating devices (FADs) in the Comoros Islands as determined by ultrasonic tagging. Aquat. Living Resour. 4: 1–12.

CAYRÉ, P., AND J. CHABANNE. 1986. Marquage acoustique et comportement de thons tropicaux (albacore: *Thunnus albacares*, et listao: *Katsuwonus pelamis*) au voisinage d'un dispositif concentrateur de poissons. Océanogr. Trop. 21: 167–183.

DERISO, R.B., R.G. PUNSLY, AND W.H. BAYLIFF. 1991. A Markov movement model of yellowfin tuna in the eastern Pacific Ocean and some analyses for international management. Fish. Res. 11: 375–395.

HAMPTON, J. 1992. Assessment of skipjack and yellowfin tuna stocks in the western tropical Pacific, using data from large-scale tagging experiments. Fifth Standing Committee on Tuna and Billfish (Honolulu, Hawaii, 18–19 June 1992). Working Paper 3. South Pacific Commission, Noumea, New Caledonia.

HILBORN, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can. J. Fish. Aquat. Sci., 47: 635–643.

HOLLAND, K.N., R.W. BRILL, AND R.K.C. CHANG. 1990. Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. Fish. Bull. (U.S.) 88: 493–507.

KLEIBER, P., A.W. ARGUE, AND R.E. KEARNEY. 1987. Assessment of Pacific skipjack tuna (*Katsuwonus pelamis*) resources by estimating standing stock and components of population turnover from tagging data. Can. J. Fish. Aquat. Sci. 44: 1122–1134.

OKUBO, A. 1980. Diffusion and ecological problems: mathematical models. Springer, New York, N.Y. 254 p.

OTTER RESEARCH. 1991. AUTODIF, a C++ array language extension with automatic differentiation for use in non-linear modeling and statistics. Otter Research Ltd., Box 265, Station A, Nanaimo, B.C. 102 p.

PRESS, W.H., B.P. FLANNERY, S.A. TEUKOLSKY, AND W.T. VETTERLING. 1988. Numerical recipes in C. Cambridge University Press, New York, N.Y. 735 p.

SIBERT, J.R., AND D.A. FOURNIER. 1993. Evaluation of diffusion–advection equations for the estimation of movement patterns from tag recapture data, p. 108–121. *In* R.S. Shomura, J. Majkowski, and S. Langi [ed.] Interactions of Pacific tuna fisheries. Proceedings of the First FAO Expert Consultation on Interaction of Pacific Tuna Fisheries, 31 December 1991, Noumea, New Caledonia. FAO Fish. Tech. Pap. No. 336/1.

SPC. 1988. Regional Tuna Tagging Project. SPC/Fisheries 20/WP.5. South Pacific Commission, Noumea, New Caledonia.

SPC. 1990. Preliminary analysis of Solomon Islands In-Country Tuna Tagging Project data. Third Standing Committee on Tuna and Billfish (Noumea, New Caledonia, 6–8 June 1990), Working Paper 4. South Pacific Commission, Noumea, New Caledonia.

Appendix A. Transfer Coefficients and Advection–Diffusion Parameters

A continuous, partial differential equation model corresponding to our tag model would be an advection–diffusion–reaction equation in two spatial dimensions (Okubo 1980) as follows:

$$\text{(A1)}\quad \frac{\partial[P]}{\partial t} = \mathcal{D}\left(\frac{\partial^2[P]}{\partial x^2} + \frac{\partial^2[P]}{\partial y^2}\right) - u\frac{\partial[P]}{\partial x} - v\frac{\partial[P]}{\partial y} + R - (M + F)[P]$$

where $[P]$ is the concentration (per unit area) of tagged fish, $\mathcal{D}$ is the diffusion parameter, u and v are easterly and northerly advection parameters, respectively, and the last two terms (recruitment minus death) constitute the reaction part of the model. The advection–diffusion part of this equation is derived (Arfken 1970, pp. 33) by considering the flow across the borders of a finite box, and then taking the limit as the box shrinks. Our discrete model is simply lifted from the derivation before the shrinking process (and then discretized with time). As such, we are considering the values of movement parameters at the borders of cells, rather than in the interior.

To see how the transfer coefficients of our discrete model relate to advection and diffusion parameters in the continuous model, let us examine a single cell boundary. In terms of our transfer coefficients, the net eastward flow across a cell boundary from cell $(i,j-1)$ to cell (i,j) would be (dropping the i index)

$$\text{(A2)}\quad \text{Net flow} = \overrightarrow{m_{j-1}}P_{j-1} - \overleftarrow{m_j}P_j$$

where P_j is the number of tagged fish in cell j and the transfer coefficients have units of time^{-1}. In terms of the diffusion and advection parameters, the flow would be

$$\text{(A3)}\quad \text{Net flow} = u_b\Delta y[P]_b - \mathcal{D}_b\Delta y\frac{\partial[P]_b}{\partial x}$$

where Δy is the size of cells in the y dimension, and subscript b indicates the boundary between cells $j-1$ and j. An approximation to $[P]_b$ would be the average concentration in the cells adjoining the boundary, that is

$$\text{(A4)}\quad [P]_b \approx \frac{1}{2}\left(\frac{P_j}{\Delta x\Delta y} + \frac{P_{j-1}}{\Delta x\Delta y}\right)$$

where Δx is the size of cells in the x dimension. The difference in concentration in the adjoining cells is an approximation of the concentration gradient, that is

$$\text{(A5)}\quad \frac{\partial[P]_b}{\partial x} \approx \frac{1}{\Delta x}\left(\frac{P_j}{\Delta x\Delta y} - \frac{P_{j-1}}{\Delta x\Delta y}\right)$$

and from Equations A3–A5, we have

$$\text{Net flow} = \frac{u_b}{2\Delta x}(P_j + P_{j-1}) - \frac{\mathcal{D}_b}{(\Delta x)^2}(P_j - P_{j-1}).$$

Regrouping leads to

$$\text{(A7)}\quad \text{Net flow} = \left(\frac{\mathcal{D}_b}{(\Delta x)^2} + \frac{u_b}{2\Delta x}\right)P_{j-1} - \left(\frac{\mathcal{D}_b}{(\Delta x)^2} + \frac{u_b}{2\Delta x}\right)P_j$$

and from inspection of Equations A2 and A7, we have the transfer coefficients in terms of the diffusion and advection parameters:

$$\text{(A8)}\quad \overrightarrow{m_{j-1}} = \frac{\mathcal{D}_b}{(\Delta x)^2} + \frac{u_b}{2\Delta x}$$
$$\overleftarrow{m_j} = \frac{\mathcal{D}_b}{(\Delta x)^2} - \frac{u_b}{2\Delta x}$$

which can be solved for the diffusion and advection parameters in terms of the transfer coefficients

$$\text{(A9)}\quad \mathcal{D}_b = (\Delta x)^2\left(\frac{\overrightarrow{m_{j-1}} + \overleftarrow{m_j}}{2}\right)$$
$$u_b = \Delta x(\overrightarrow{m_{j-1}} - \overleftarrow{m_j}).$$

Similar results hold for north–south movement. The spatially varying diffusion coefficient $\mathcal{D}$ given here for a continuous model should not be confused with the constant diffusion parameter D in the discrete model — hence the different symbols. Although they are related, they are not the same.

Appendix B. Derivation of Formula for FAD Factor

Although the following derivation makes simplifying and somewhat vague assumptions about how FADs might affect the tendency of fish to exit a cell, it does give some theoretical justification for the mathematical form of the formula we used for FAD effect. It also allows us to relate the parameter f_h estimated by the model to the distance over which a single FAD might exert its effects.

Define μ to be the transfer coefficient in some direction out of a cell, assuming that there are no FADs in the cell. To get the effective transfer coefficient when there are f FADs in the cell, μ would be modified by the FAD effect, $\phi(f)$, as in Equations 2. Thus the suitably modified transfer coefficient would be given by

$$\text{(B1)}\quad m_f = \mu\phi(f).$$

Our aim is to derive a formula for the function $\phi(f)$.

If a FAD exerts its effects over a region of size a, and if a cell is of size A, then, assuming $a < A$, the proportion of a cell that is influenced by a single FAD is

$$\text{(B2)}\quad p_1 = \frac{a}{A}$$

and the proportion not influenced by that FAD is $1 - p_1$. If we assume for the moment that f FADs are randomly distributed in a cell such that regions of influence may or may not overlap, then the expected proportion of the cell not influenced by any FADs would be $(1 - p_1)^f$, and the complementary expected proportion of the cell influenced by one of more of the FADs is

$$\text{(B3)}\quad p_f = 1 - (1 - p_1)^f = 1 - e^{\ln(1-p_1)f}.$$

If fish under the influence of FADs have their mobility reduced in such a way that their tendency to exit the cell is s times the tendency for uninfluenced fish, and if fish are randomly disposed within the cell (recall that the cell is the limit of spatial resolution in the model), then for f FADs in a cell, the number fish exiting in some direction per unit time is the sum of the exit rates from influenced and uninfluenced fish, that is

(B4) Exit rate = $s\mu p_f P + \mu(1 - p_f)P = \mu[1 - (1 - s)p_f]P$

where P is the population of fish in the cell. Because the effective transfer coefficient, m_f, is the proportion of fish in the cell exiting per unit time, Equation B4 implies that m_f should be given by

(B5) $m_f = \mu[1 - (1 - s)p_f]$

and from Equation B1,

(B6) $\phi(f) = 1 - (1 - s)p_f$

which, substituting from Equation B3 and simplifying, gives

(B7) $\phi(f) = s + (1 - s)e^{\ln(1-p_1)f}$.

The half-saturation parameter, f_h, is the number of FADs at which half the saturated FAD effect is realized, that is

(B8) $e^{\ln(1-p_1)f_h} = \frac{1}{2}$

from which Equation B7 becomes

(B9) $\phi(f) = s + (1 - s)e^{-\frac{\ln(2)}{f_h}f}$

which is Equation 3 in the main text of this paper without the cell indices.

The assumption of random placement of FADs is certainly not strictly true. The opposite extreme would be precise equidistant placement, which would lead to ϕ as a linear function of f up to the saturation point, after which it would be constant at that level. The reality is presumably somewhere in between. We made the assumption of randomness to avoid the discontinuity of the equidistant result which could cause difficulties in the fitting procedure. Another parameter could be added to the expression for ϕ to give a result between equidistant and random, but in the interest of parameter parsimony, we have not done so.

Appendix C. Radius of FAD Action

We can relate f_h, estimated by the model, to the radius of FAD action. From Equations B2 and B8 in Appendix B, we get the region of action of a single FAD,

$$a = A\left[1 - \left(\frac{1}{2}\right)^{1/f_h}\right]$$

assuming the FADs are randomly placed in the cell. If the region of action is circular, then

(C1) $r = \sqrt{\frac{a}{\pi}} = \sqrt{\frac{A}{\pi}\left[1 - \left(\frac{1}{2}\right)^{1/f_h}\right]}$

is the radius of action implied by an estimate of f_h.

Of course the FADs are not really randomly placed in the cells (Fig. 1). In fact in some instances they seem to lie in a transect across the cell. Our data resolution is not adequate to deal effectively with the arrangements within a cell, but if we assume that the FADs are randomly placed along a line across the cell and assume further that the fish are concentrated near that line, then an argument similar to the above leads to

(C2) $r = \frac{1}{2}L\left[1 - \left(\frac{1}{2}\right)^{1/f_h}\right]$

as the radius of FAD action, where L is the length of the transect.

Confounding of Gear Selectivity and the Natural Mortality Rate in Cases where the Former is a Nonmonotone Function of Age

Grant G. Thompson

United States Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, Resource Ecology and Fisheries Management Division, 7600 Sand Point Way NE, Seattle, WA 98115-0070, USA

Thompson, G.G. 1994. Confounding of gear selectivity and the natural mortality rate in cases where the former is a nonmonotone function of age. Can. J. Fish. Aquat. Sci. 51: 2654–2664.

An "exponential–logistic" selectivity function is presented in which a single parameter (γ) determines whether gear selectivity is asymptotic ($\gamma = 0$) or reaches a maximum at finite age ($\gamma > 0$). The function is used to develop a model in which both γ and the natural mortality rate M are formally indeterminate and in which the coming year's catch limit can be viewed as a response function of either estimated γ or estimated M. Decision theory is then used to derive the optimal catch. The optimal catch is shown to increase with the degree of uncertainty surrounding M, although this conclusion may depend on the short managerial time frame assumed. Three "suboptimal" strategies are also considered: (1) setting catch at the level corresponding to the expected value of M, (2) setting catch at the minimum of the response function, and (3) setting catch at the level corresponding to $\gamma = 0$. The first suboptimal strategy never results in a catch greater than the optimum and always results in a lower expected loss than the second. The performance of the third strategy (relative to the others) depends on parameter values.

On présente dans cet article une fonction de sélectivité « exponentielle–logistique » dans laquelle un seul paramètre (γ) détermine si la sélectivité d'un engin est asymptotique ($\gamma = 0$) ou atteint un maximum à un âge fini ($\gamma > 0$). Cette fonction est utilisée pour l'élaboration d'un modèle dans lequel γ et le taux naturel de mortalité (M) sont tous deux laissés formellement indéterminés et la limite de prises de l'année à venir peut être vue comme une fonction de réponse de la valeur estimée de γ ou de M. On recourt ensuite à la théorie des décisions pour établir le taux de capture optimal. Ce dernier augmente avec le degré d'incertitude entourant M, quoique cette conclusion peut dépendre de la courte période de gestion envisagée. Trois stratégies « suboptimales » sont également présentées : 1) établissement des prises au niveau correspondant à valeur prévue de M, 2) établissement des prises au minimum de la fonction de réponse et 3) établissement des prises au niveau correspondant à $\gamma = 0$. Avec la première, on obtient un taux de capture jamais supérieur à l'optimum, et les pertes attendues sont toujours inférieures à celles obtenues avec la deuxième. La performance de la troisième stratégie, relativement à celle des autres, dépend des valeurs des paramètres.

Received March 1, 1994
Accepted October 4, 1994
(J12294)

Reçu le 1er mars 1994
Accepté le 4 octobre 1994

It is generally understood that the instantaneous rate of natural mortality M is difficult to estimate from catch-at-age data alone (Doubleday 1976), requiring instead some sort of auxiliary information (Paloheimo 1980; Fournier and Archibald 1982; Fournier 1983; Deriso et al. 1985, 1989; Thompson and Bakkala 1990). More specifically, for the case in which selectivity is constrained to increase continuously as a function of age (i.e., if selectivity is monotone), it has been demonstrated that auxiliary data can enable estimation of both M and the parameters governing the selectivity schedule (Fournier and Archibald 1982, Fournier 1983). However, the same conclusion has apparently not been demonstrated for the alternative case in which selectivity is allowed to be a nonmonotone function of age.

This raises a number of concerns, as incorrect or uncertain estimates of M have been shown to cause serious errors in a variety of stock assessment outputs, including estimates of the fishing mortality rate F, year class strength, and overall stock size (Agger et al. 1973; Ulltang 1977; Sims 1984; Sampson 1987; Hilden 1988; Lapointe et al. 1989). Curiously, the effects of incorrect or uncertain estimates of M on appropriate harvest levels have received relatively scant attention. Pope (1983) showed that appropriate harvest levels are largely unaffected by errors in M for the special case in which the management objective is to maintain F at its current level. Hilden (1988) reported that the ICES Working Group on Methods for Fish Stock Assessments had taken Pope's argument further, suggesting that the insensitivity of forecasted harvest levels to errors in estimated M is a fairly general phenomenon. It seems appropriate that this claim be investigated because its generality (or lack thereof) has profound implications for how fishery management advice should be provided.

The purpose of this paper, then, is to investigate the relationship between estimates of M and the selectivity schedule (more precisely, the *survey* selectivity schedule) and to evaluate alternative catch levels in light of that relationship. The approach is as follows. First, a theoretical model is developed in which one parameter of the selectivity function and M are formally indeterminate and in which the catch corresponding to the intended harvest strategy varies dramatically with either of these parameters. Second,

Bayesian decision theory is used to solve numerically for the optimal harvest level. Third, an approximation to the theoretical model is presented, an analytic solution for the optimal catch level derived, and its behavior explored. Fourth, three "suboptimal" catch levels are evaluated.

An Example of Indeterminacy

Central Features

An illustration of indeterminacy in the estimation of selectivity and M may be developed around the following features.

(1) A stock in equilibrium under some initial total mortality rate Z_0, with dynamics above some minimum age x_r governed without error by equations of known functional form.

(2) An assessment survey which is known to measure the *relative* age composition (as filtered through a selectivity schedule) without error, and which is known to measure the *absolute* abundance at some (unknown) age without error.

(3) An errorless measurement of total catch (in weight).

(4) A harvest strategy based on fishing at an instantaneous rate which would maintain, in equilibrium, an intended relative level of spawning per recruit (SPR).

It should be stressed that the above features are intended only for the purpose of developing an illustration of the alleged indeterminacy, and are by no means suggested to constitute a completely general description either of fishery resources or of the stock assessment process.

Selectivity in the Stock Assessment Survey

Turning first to the second feature listed above, it will be assumed that survey selectivity S is a function of age following the "exponential–logistic" form suggested by Thompson and Bakkala (1990). This curve takes its name from the fact that it can be viewed as the product of a negative exponential term and a logistic term, scaled so that the value at the peak is unity:

$$(1)\qquad S(x)=\left(\frac{1}{1-\gamma}\right)\left(\frac{1-\gamma}{\gamma}\right)^{\gamma}\left(\frac{e^{\alpha\gamma(\beta-x)}}{1+e^{\alpha(\beta-x)}}\right)$$

where α, β, and γ are all positive constants. Sample curves are shown in Fig. 1. Equation (1) exhibits a peak at

$$(2)\qquad x_p=\left(\frac{1}{\alpha}\right)\ln\left(\frac{1-\gamma}{\gamma}\right)+\beta$$

and inflection points at

$$(3)\qquad x_1=\left(\frac{1}{\alpha}\right)\ln\left(\frac{2-4\gamma+2\gamma^2}{(1+2\gamma-2\gamma^2)+\sqrt{1+4\gamma-4\gamma^2}}\right)+\beta$$

and

$$(4)\qquad x_2=\left(\frac{1}{\alpha}\right)\ln\left(\frac{2-4\gamma+2\gamma^2}{(1+2\gamma-2\gamma^2)-\sqrt{1+4\gamma-4\gamma^2}}\right)+\beta.$$

The heights at the inflection points are prescribed wholly by γ, with $S(x_1)$ and $S(x_2)$ given respectively by

$$(5)\qquad S_1=\frac{\left(\dfrac{1+\sqrt{1+4\gamma-4\gamma^2}}{2\gamma(1+\gamma)}+1\right)^{\gamma}}{\dfrac{1+\sqrt{1+4\gamma-4\gamma^2}}{2=(1+\gamma)}+1}$$

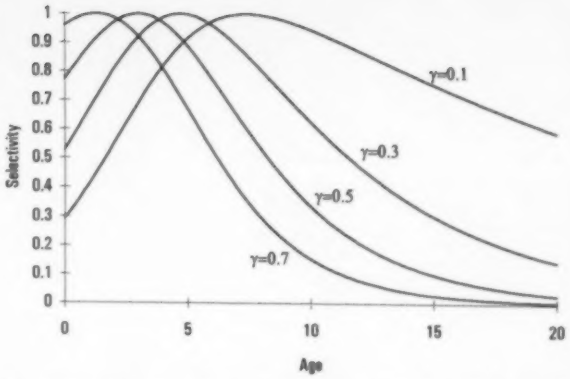


FIG. 1. Sample selectivity curves (Equation (1)) under various levels of selectivity parameter γ. For all curves, selectivity parameters α and β have been fixed at values of 1/2 and 3, respectively.

and

$$(6)\qquad S_2=\frac{\left(\dfrac{1-\sqrt{1+4\gamma-4\gamma^2}}{2\gamma(1+\gamma)}+1\right)^{\gamma}}{\dfrac{1-\sqrt{1+4\gamma-4\gamma^2}}{2(1+\gamma)}+1}.$$

Clearly, the exponential–logistic curve contains the traditional logistic curve as a special case as γ approaches zero. By adding a third parameter (γ), the exponential–logistic curve generalizes the logistic curve to cover cases in which selectivity is nonmonotone. Less obviously, the exponential–logistic curve is a special case of the four-parameter "double logistic" curve introduced by Methot (1990), which has become a fairly common tool for describing selectivity patterns (e.g., Bence et al. 1993, Sampson 1993). Unfortunately, the double logistic cannot be written in a form which automatically scales the peak to a value of unity. The exponential–logistic thus represents an intermediate form which retains the tractability of the logistic while sacrificing little of the flexibility found in the double logistic. The derivation of the exponential–logistic as a special case of the double logistic is given in Appendix A.

Estimation of Numbers-at-Age

Numbers n at age x are given for the initial equilibrium state by

$$(7)\qquad n(x)=Re^{-Z_0(x-x_r)}$$

where R is the recruitment level, measured in numbers of fish at age x_r. Note that this formulation implies that all ages above x_r are impacted equally by F; in other words, commercial selectivity is unity for all recruited ages. This assumption obviously contrasts with the assumption of age-dependent survey selectivity (Equation (1)), and could certainly be relaxed if desired. However, because the assumption of knife-edge recruitment to the commercial fishery simplifies the analysis greatly and does not impair the model's ability to address the objectives of the present paper, it shall be retained here.

Survey numbers at age $n_s(x)$ are then given by the product of actual numbers $n(x)$ and survey selectivity $S(x)$:

$$(8)\quad n_s(x) = n(x)S(x)$$

$$= Re^{-Z_0(x-x_r)}\left(\frac{1}{1-\gamma}\right)\left(\frac{1-\gamma}{\gamma}\right)^{\gamma}\left(\frac{e^{\alpha\gamma(\beta-x)}}{1+e^{\alpha(\beta-x)}}\right).$$

Let the estimated value of γ be designated $\hat{\gamma}$ (the convention of using a "circumflex" symbol to denote estimated values will be used throughout this paper). Substituting $\hat{\gamma}$ for γ in Equation (1) then gives the equation for estimated selectivity $\hat{S}(x)$. Dividing survey numbers at age x_r (Equation (8) evaluated at $x = x_r$) by estimated selectivity at age x_r then gives estimated recruitment, which can be thought of as a function of estimated γ, $\hat{R}(\hat{\gamma})$:

$$(9)\quad \hat{R}(\hat{\gamma}) = R\left(\frac{1-\gamma}{\gamma}\right)^{\gamma}\left(\frac{\hat{\gamma}}{1-\hat{\gamma}}\right)^{\hat{\gamma}}\left(\frac{1-\hat{\gamma}}{1-\gamma}\right)e^{\alpha(\gamma-\hat{\gamma})(\beta-x_r)}.$$

Then, substituting Equation (9) for R, $\hat{\gamma}$ for γ, and $\hat{Z}_0$ for Z_0 in Equation (8) gives an alternative form for survey numbers-at-age:

$$(10)\quad n_s(x) = \hat{R}(\hat{\gamma})e^{-\hat{Z}_0(x-x_r)}\left(\frac{1}{1-\hat{\gamma}}\right)\left(\frac{1-\hat{\gamma}}{\hat{\gamma}}\right)^{\hat{\gamma}}\left(\frac{e^{\alpha\hat{\gamma}(\beta-x)}}{1+e^{\alpha(\beta-x)}}\right).$$

Since survey numbers are observed directly, any values for $\hat{\gamma}$ and $\hat{Z}_0$ inserted into Equation (10) must produce a function identical to Equation (8). Equating the right-hand sides of these two expressions and solving for $\hat{Z}_0$ gives

$$(11)\quad \hat{Z}_0(\hat{\gamma}) = Z_0 + \alpha(\gamma - \hat{\gamma}).$$

Equation (11) implies that estimates of Z_0 and γ will be linearly and inversely related (paralleling a result obtained by Deriso et al. (1985, 1989)). Because the only directly observable quantity in this example (other than total catch) is the survey age composition, and because the estimated survey age composition is invariant for any $\hat{\gamma}$ (given that $\hat{Z}_0(\hat{\gamma})$ falls out according to Equation (11)), Z_0 and γ are formally indeterminate in this example.

Assuming that negative estimates of Z_0 are inadmissible, estimates of γ are constrained (from above) by the lesser of 1 and the value which sets $\hat{Z}_0(\hat{\gamma})$ equal to 0:

$$(12)\quad \gamma_{max} = \min\left(\frac{Z_0}{\alpha} + \gamma, 1\right).$$

Estimation of Stock Biomass, Mortality Rates, and Intended Catch

In terms of stock biomass, the simple dynamic pool model with linear growth described by Hulme et al. (1947) and Thompson (1992a) will be assumed. In addition to the assumptions listed above, other important features of the model include continuous cohort dynamics, an infinite maximum age, and a linear weight-at-age relationship. Given these assumptions, initial stock biomass B_0 is estimated as

$$(13)\quad \hat{B}_0(\hat{\gamma}) = \hat{R}(\hat{\gamma})w_r\left(\frac{\hat{Z}_0(\hat{\gamma}) + \delta}{\hat{Z}_0(\hat{\gamma})^2}\right)$$

where w_r is mean body weight at age x_r and δ is the reciprocal of the difference between x_r and the age intercept of the weight-at-age relationship.

Because this is a simple dynamic pool model, the fishing mortality rate in the initial equilibrium (F_0) is just the ratio of (observed) initial catch Y_0 to initial biomass, meaning that estimated F_0 can be written as the following function of $\hat{\gamma}$:

$$(14)\quad \hat{F}_0(\hat{\gamma}) = \frac{Y_0}{\hat{B}_0(\hat{\gamma})}$$

in which case, estimated M can be written

$$(15)\quad \hat{M}(\hat{\gamma}) = \hat{Z}_0(\hat{\gamma}) - \hat{F}_0(\hat{\gamma}) = M + F_0 - \hat{F}_0(\hat{\gamma}) + \alpha(\gamma - \hat{\gamma}).$$

Important special cases of Equation (15) are the estimated values of M corresponding to $\hat{\gamma} = 0$ and $\hat{\gamma} = \gamma_{max}$, which are

$$(16)\quad \hat{M}_{max} = \alpha\gamma + Z_0 - \frac{Y_0(1-\gamma)e^{-\alpha\gamma(\beta-x_r)}}{Rw_r\left(\frac{1-\gamma}{\gamma}\right)^{\gamma}\left(\frac{\alpha\gamma + Z_0 + \delta}{(\alpha\gamma + Z_0)^2}\right)}$$

and

$$(17)\quad \hat{M}_{min} = \max\left((\alpha(\gamma-1) + Z_0)\right.$$

$$\left.\times\left[1 - \frac{Y_0(1-\gamma)e^{-\alpha(\gamma-1)(\beta-x_r)}}{Rw_r\left(\frac{1-\gamma}{\gamma}\right)^{\gamma}\left(\frac{\delta}{\alpha(\gamma-1)+Z_0} + 1\right)}\right], 0\right),$$

respectively.

A couple of conventions should be noted in light of Equations (16) and (17). First, because it will often prove convenient to normalize parameters by scaling them relative to $\hat{M}_{max}$, the symbol r will preface any parameter that has been scaled in this manner (e.g., $rX \equiv X/\hat{M}_{max}$)). Second, to simplify the remainder of the argument, it will be assumed from this point on that M, F_0, α, and γ have values such that $\gamma_{max} < 1$, in which case $\hat{M}_{min} = 0$.

Currently, a common management strategy is to set catches by using a fishing mortality rate which corresponds to some equilibrium level of lifetime spawning per recruit, usually expressed as a percentage of the pristine level (Goodyear 1977, 1993; Clark 1991; Mace and Sissenwine 1993). For the present model (where the level of spawning is assumed proportional to total stock biomass), the fishing mortality rate corresponding to a specified level of spawning per recruit can be calculated as

$$(18)\quad F(\hat{\gamma})$$

$$= M(\hat{\gamma})\left(\frac{M(\hat{\gamma}) + \sqrt{4\mathrm{SPR}\delta(\delta + M(\hat{\gamma})) + M(\hat{\gamma})^2}}{2\mathrm{SPR}(\delta + M(\hat{\gamma}))} - 1\right)$$

where SPR is the relative level of spawning per recruit (Thompson 1993).

Again, because this is a simple dynamic pool model (Thompson 1992a), recruitment is a deterministic function of parent stock biomass alone (spawning is assumed proportional to stock biomass), meaning that recruitment throughout the coming x_r years will be constant at the initial equilibrium level. More particularly, recruitment during the coming year will be constant at the initial equilibrium level

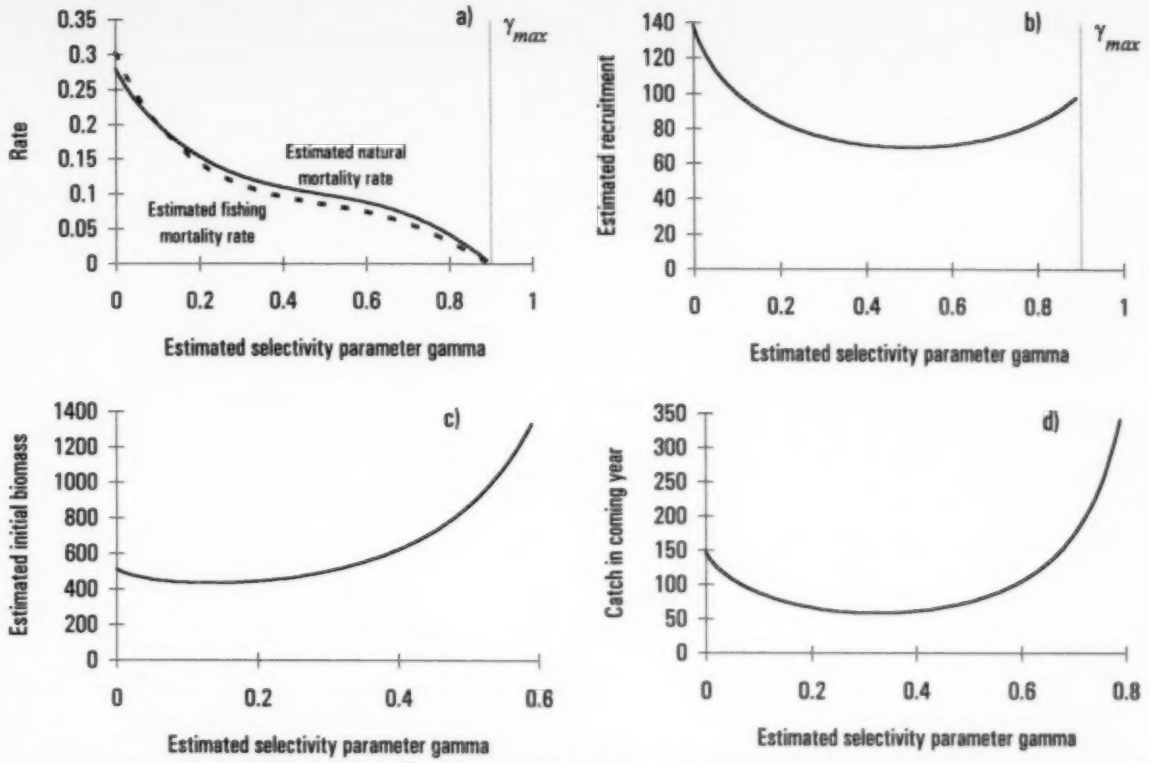


FIG. 2. Model outputs graphed as functions of $\hat{\gamma}$, the estimated value of one of the three parameters used to define selectivity (Equation (1)). In each of the bottom two panels, the curve reaches a vertical asymptote at $\hat{\gamma} = \gamma_{max}$.

so long as $x_r \geq 1$. This implies that yield in the coming year would likewise remain at the initial equilibrium level Y_0 if the coming year's F were set equal to F_0. More generally, however, yield in the coming year will follow the relationship derived in Appendix B and shown below:

$$(19)\quad Y(\hat{\gamma}) = \hat{R}(\hat{\gamma})w_r\left[\left(\frac{\hat{F}(\hat{\gamma})}{\hat{Z}(\hat{\gamma})}\right)\left[\left(\frac{\delta}{\hat{Z}(\hat{\gamma})}+1\right)\right.\right.$$
$$\left. + \hat{s}(\hat{\gamma})\left(\frac{\delta}{\hat{Z}(\hat{\gamma})} - \frac{\delta}{\hat{Z}_0(\hat{\gamma})}\right)\right] + \hat{u}(\hat{\gamma})\left[\left(\frac{1}{\hat{Z}_0(\hat{\gamma})}\right)\left(\frac{\delta}{\hat{Z}(\hat{\gamma})}\right.\right.$$
$$\left.\left. + \frac{\delta}{\hat{Z}_0(\hat{\gamma})}+1\right) - \left(\frac{1}{\hat{Z}(\hat{\gamma})}\right)\left(\frac{2\delta}{\hat{Z}(\hat{\gamma})}+1\right)\right]\Bigg]$$

where the total instantaneous mortality rate (estimated) is given by $\hat{Z}(\hat{\gamma}) = \hat{M}(\hat{\gamma}) + \hat{F}(\hat{\gamma})$, the discrete survival rate (estimated) is given by $\hat{s}(\hat{\gamma}) = e^{-\hat{Z}(\hat{\gamma})}$, and Baranov's exploitation rate (estimated) is given by $\hat{u}(\hat{\gamma}) = \hat{F}(\hat{\gamma})(1 - \hat{s}(\hat{\gamma}))/\hat{Z}(\hat{\gamma})$.

With help from the above equations, the relationships between $\hat{\gamma}$ and many variables of interest can be examined with ease. Figure 2 shows an example of how estimated M, F, R, B_0, and Y all vary as functions of $\hat{\gamma}$, corresponding to the parameter values listed in Table 1. It should be stressed that in conducting an actual stock assessment, curves such as those shown in Fig. 2 would be constructed by plotting the results of a large number of runs from the assessment model (a version of virtual population analysis, or something of that nature), each with $\hat{\gamma}$ fixed at a different value. That is, the assessment scientist could not simply plot the equations per se (as has been done here) because these typically depend on the true value of γ, which is unknown. In other words, the equations are presented here for the purpose of describing the mechanisms reflected in the results of a stock assessment, not to describe the process of the stock assessment itself.

Salient features of Fig. 2 include the following. Estimated M and estimated F (Fig. 2a) tend to be very close in this example (they are identical at $\hat{\gamma} = \gamma$, although this is true in general for an SPR of 35% only when $\delta = 3M/2$). Estimated M decreases monotonically from a value of $\hat{M}_{max}$ at $\hat{\gamma} = 0$ (the logistic case) to a value of zero at $\hat{\gamma} = \hat{\gamma}_{max}$. Estimated recruitment declines from an initial high level at $\hat{\gamma} = 0$ to a minimum at $\hat{\gamma} = (1 + e^{-\alpha(\beta - x_r)})^{-1}$, after which it again increases with $\hat{\gamma}$ to a terminal value at $\hat{\gamma} = \hat{\gamma}_{max}$ (Fig. 2b). Estimated initial biomass (Fig. 2c) and yield for the coming year (Fig. 2d) also exhibit minimum values, but both increase to a vertical asymptote at $\hat{\gamma} = \hat{\gamma}_{max}$.

Computing the Decision–Theoretic Optimum

In light of Fig. 2d, the appropriate response to the demonstrated indeterminacy of γ and M depends in part on the nature of the "intended" catch level. Generally speaking, this catch level is meant to represent the harvest limit which one would impose if the true value of γ (or, alternatively, M) were known. However, within this general definition a number of interpretations are possible. For example, the intended

TABLE 1. Parameter values used in example.

Parameter	Value	Interpretation
Parameters used in the selectivity function and simple dynamic pool model		
α	0.5	Selectivity parameter
β	3	Selectivity parameter
γ	0.1	Selectivity parameter
δ	0.3	Growth parameter
F_0	0.2	Initial instantaneous fishing mortality rate
M	0.2	Instantaneous natural mortality rate
R	100	Recruitment (in numbers)
SPR	0.35	Relative level of spawning per recruit
x_r	3	Age of knife-edge recruitment to the fishery
Parameters used to define the probability density function of M		
rm	0.5	Relative mean (absolute mean divided by $\hat{M}_{max}$)
CV	0.3	Coefficient of variation

catch might be viewed as something like the upper bound of the "safe" region, that is, a catch level above which the stock's long-term productive capacity is jeopardized (as in the U.S. National Marine Fisheries Service definition of overfishing, Thompson 1993). In this case, one's objective might be to minimize the chance of exceeding the intended catch, implying that setting catch at the minimum point of Fig. 2d would be appropriate.

On the other hand, setting catch at the minimum point of Fig. 2d may be too conservative if the intended catch is viewed instead as something like a desired (or optimal) level. If the SPR used to compute the intended catch level incorporates a reasonable margin for error (i.e., if exceeding the intended catch for a short time does not jeopardize the stock's long-term productive capacity), a logical way to approach the problem would be to employ Bayesian decision theory (e.g., DeGroot 1970), wherein the objective is to minimize the expected loss resulting from a management decision. This approach requires first that the uncertain parameter(s) in the problem be identified. Here, either γ or M could be chosen because each can be written (perhaps implicitly) as a function of the other. For the time being, let γ represent the single unknown parameter in the system.

Next, it is necessary to choose a loss function describing the costs associated with alternative outcomes (perhaps normalized so that zero costs are associated with the true target catch). If the intended level of SPR has been chosen conservatively so that exceeding the true target catch by reasonable amounts is unlikely to jeopardize the stock's long-term productive capacity, a symmetric loss function would be reasonable, that is, a loss function in which underestimating the true target catch is just as costly (to society) as overestimating the true target catch by the same amount. A convenient choice for a symmetric loss function is the quadratic, which can be written

$$(20)\quad L(\gamma,\hat{\gamma}) = (Y(\gamma) - Y(\hat{\gamma}))^2.$$

The final component required for implementing the Bayesian approach is a density function describing the probability of different values of γ. Unfortunately, it seems unlikely that the stock assessment scientist will have much prior knowledge regarding the probability density function (pdf) of γ per se. However, it does seem reasonable to assume that the assessment scientist will have some prior knowledge regarding the pdf of M based on life history information or published estimates for similar stocks or species. Because the range of possible values for M is bounded in this model (M can range between zero and $\hat{M}_{max}$), a convenient choice for the pdf of M is the beta distribution, which can be written

$$(21)\quad p(M) = \left(\frac{\Gamma(a+b)}{\Gamma(a)\Gamma(b)}\right)\left(\frac{1}{\hat{M}_{max}}\right)\left(\frac{M}{\hat{M}_{max}}\right)^{a-1}\left(1-\frac{M}{\hat{M}_{max}}\right)^{b-1}$$

where $\Gamma(\cdot)$ is Euler's gamma function, and a and b are parameters which can be defined in terms of the relative mean rm (i.e., the absolute mean m scaled relative to $\hat{M}_{max}$) and coefficient of variation CV as follows:

$$(22)\quad a = \left(\frac{1-\mathrm{rm}}{\mathrm{rm}\,\mathrm{CV}^2} - 1\right)\mathrm{rm}$$

and

$$(23)\quad b = \left(\frac{1-\mathrm{rm}}{\mathrm{rm}\,\mathrm{CV}^2} - 1\right)(1-\mathrm{rm}).$$

Figure 3a shows a sample pdf corresponding to parameters rm = 0.5 and CV = 0.3.

To convert Equation (21) into a pdf of γ, first note that Equation (15) gives estimated M as a function of estimated γ, with derivative

$$(24)\quad \frac{d\hat{M}}{d\hat{\gamma}} = \frac{Y_0\left(\left[\ln\left(\frac{\hat{\gamma}}{1-\hat{\gamma}}\right) - \alpha(\beta - x_r)\right](\alpha(\gamma-\hat{\gamma}) + Z_0 + \delta) - \alpha\left[\frac{2\delta}{\alpha(\gamma-\hat{\gamma}) + Z_0} + 1\right]\right)}{Rw_r\left(\frac{1-\gamma}{\gamma}\right)^{\gamma}\left(\frac{\hat{\gamma}}{1-\hat{\gamma}}\right)^{\hat{\gamma}}\left(\frac{1-\hat{\gamma}}{1-\gamma}\right)e^{\alpha(\gamma-\hat{\gamma})(\beta-x_r)}\left(\frac{\delta}{\alpha(\gamma-\hat{\gamma}) + Z_0}\right)^2} - \alpha.$$

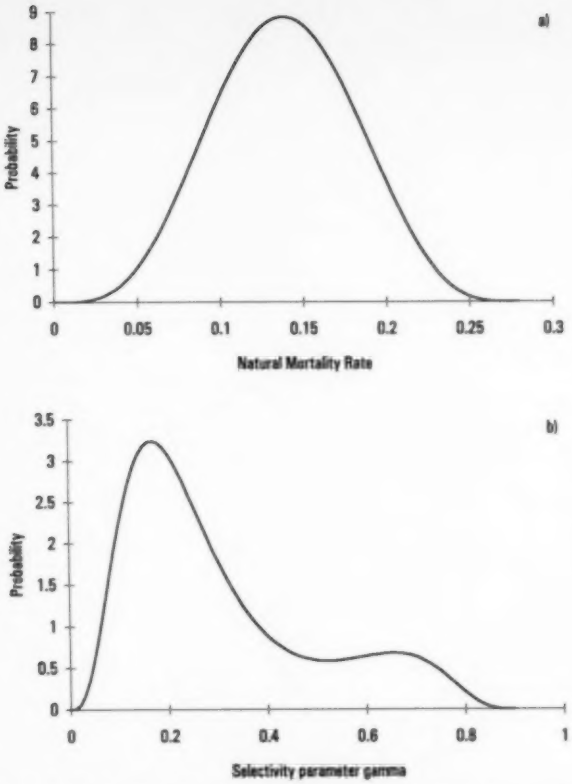


FIG. 3. Probability density functions of (a) the natural mortality rate M and (b) selectivity parameter γ.

Following the standard technique for transformation of continuous random variables (e.g., Hogg and Craig 1970), and assuming that the function $\hat{M}(\hat{\gamma})$ is monotone, the pdf of γ can then be estimated by substituting Equations (15) and (24) into the following:

$$(25)\quad q(\gamma) = p(\hat{M}(\hat{\gamma}))\left|d\hat{M}/d\hat{\gamma}\right|.$$

Figure 3b shows a sample pdf corresponding to the parameters shown in Table 1. Note that the pdf in this figure is bimodal, despite the fact that the pdf from which it is derived (Fig. 3a) is unimodal.

The expected loss associated with any given choice of $\hat{\gamma}$ is then

$$(26)\quad \mathrm{EL}(\hat{\gamma}) = \int_0^{\gamma_{\max}} L(\gamma, \hat{\gamma}) q(\gamma) d\gamma.$$

Figure 4 shows how expected loss varies with $\hat{\gamma}$ for the parameters shown in Table 1.

The decision-theoretic solution is the value of $\hat{\gamma}$ which minimizes Equation (26). For the parameters shown in Table 1, Equation (26) is minimized at values of 0.108 and 0.545, corresponding to estimated M values of 0.195 and 0.094, respectively (Fig. 4). Figure 4 also indicates that the objective function has a local maximum at a $\hat{\gamma}$ value of 0.324, which corresponds to the minimum of the catch response function (Fig. 2d). The local maximum in Fig. 4 corresponds to an estimated M of 0.121. The value of the objective function at either of the minima is 2905, increasing to 3635 at the local maximum and to 6688 at $\hat{\gamma} = 0$ ($\hat{M} = \hat{M}_{\max}$).

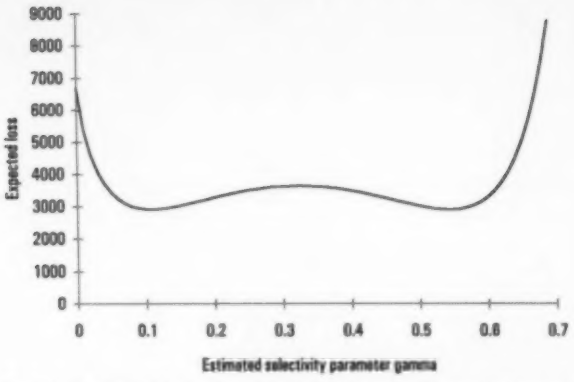


FIG. 4. Expected loss as a function of the estimated value of selectivity parameter γ.

For comparison, a $\hat{\gamma}$ of 0.243 corresponds to an estimated M equal to the mean of Equation (21) and an expected loss of 3470. Thus, in this example, setting M equal to the mean of the pdf would not be optimal, but would result in a lower expected loss than setting catch equal to the minimum of the response function (Fig. 2d).

An Approximation to the Decision-Theoretic Solution

Because finding the minimum of Equation (26) is a computationally intensive process, and a rather opaque one at that, a simple approximation can provide some insight into the behavior of the full decision–theoretic solution. To begin with, the profile of yield versus $\hat{\gamma}$ in Fig. 2d shows three central features: an intercept at $\hat{\gamma} = 0$, a minimum at some intermediate value of $\hat{\gamma}$, and an asymptote at $\hat{\gamma} = \gamma_{\max}$. The solid curve in Fig. 5 shows yield for the same system, but plotted instead against estimated natural mortality rate $\hat{M}$ (since both yield and $\hat{M}$ are functions of $\hat{\gamma}$, either can be plotted in terms of the other, with $\hat{\gamma}$ implicit). The solid curve in Fig. 5 shows the same pattern as Fig. 2d, but reversed: an asymptote at $\hat{M} = 0$, a minimum at some intermediate value of $\hat{M}$, and a terminal value at $\hat{M} = \hat{M}_{\max}$. A simple function exhibiting the same central features is

$$(27)\quad Y(\hat{M}) = \frac{k_2}{\hat{M}^2} + k_1\hat{M}^2 + k_0$$

where the k_i are positive constants. To approximate the solid curve shown in Fig. 5, define the k_i as shown below:

$$k_0 = \frac{\left[1 + \left(\frac{\hat{M}^*}{\hat{M}_{\max}}\right)^4\right] Y^* - 2\left(\frac{\hat{M}^*}{\hat{M}_{\max}}\right)^2 Y_{\max}}{\left[1 - \left(\frac{\hat{M}^*}{\hat{M}_{\max}}\right)^2\right]^2}$$

$$k_1 = \frac{Y_{\max} - Y^*}{\hat{M}_{\max}^2\left[1 - \left(\frac{\hat{M}^*}{\hat{M}_{\max}}\right)^2\right]^2}$$

and

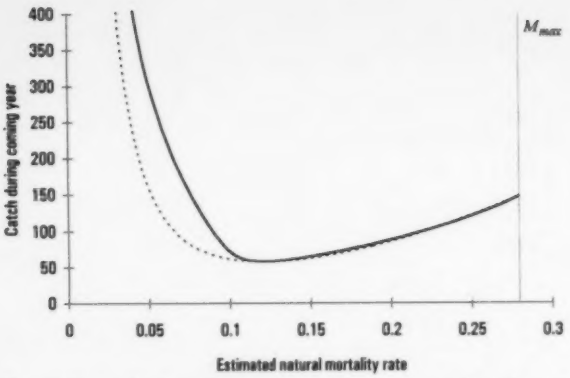


FIG. 5. Prescribed catch for the coming year as a function of the estimated natural mortality rate $\hat{M}$. The solid curve denotes the response function from the full model, while the dashed curve denotes the approximation from Equation (27).

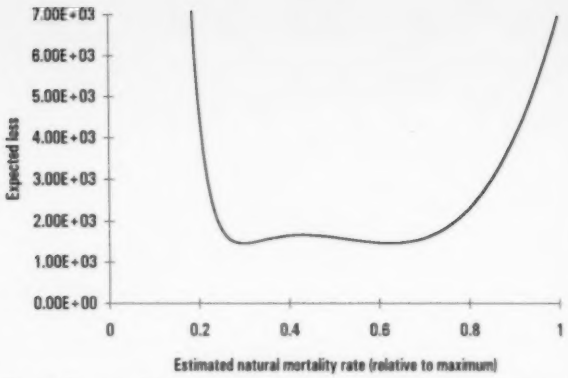


FIG. 6. Expected loss in the approximation (Equation (30)) as a function of the estimated natural mortality rate (scaled relative to the maximum, $\hat{M}_{max}$).

$$k_2 = \frac{\hat{M}^{*4}(Y_{max} - Y^*)}{\hat{M}_{max}^2\left[1 - \left(\frac{\hat{M}^*}{\hat{M}_{max}}\right)^2\right]^2}$$

where $\hat{M}^*$ is the value of $\hat{M}$ at which the solid curve in Fig. 5 is minimized, Y^* is the value of Y corresponding to $\hat{M}^*$, and Y_{max} is the value of Y corresponding to M^*_{max}. Setting the k_i in this manner forces the minima of the "true" and approximated curves to coincide, along with their terminal points (at $\hat{M} = \hat{M}_{max}$). The approximated relationship (Equation (27)) corresponds to the dashed curve shown in Fig. 5.

Now that the expression for Y (Equation (27)) has been cast in terms of $\hat{M}$ rather than $\hat{\gamma}$, the loss function (Equation (20)) can be rewritten in terms of M and $\hat{M}$, and Equation (21) can be used directly in the computation of expected loss instead of the more complicated Equation (25). The loss function becomes

$$(28)\quad L(M,\hat{M}) = (Y(M) - Y(\hat{M}))^2$$

and the expression for expected loss is

$$(29)\quad \mathrm{EL}(\hat{M}) = \int_0^{\hat{M}_{max}} L(M,\hat{M})p(M)dM.$$

Conveniently, the forms of Equations (27) and (21) permit analytical solution of Equation (29), namely:

$$(30)\quad \mathrm{EL}(r\hat{M}) = k_1^2\hat{M}_{max}^4\begin{pmatrix} r\hat{M}^4 - \\ 2(\mu_2 r\hat{M}^{*4} + \mu_1)r\hat{M}^2 + \\ (\mu_3 r\hat{M}^{*8} + 4r\hat{M}^{*4} + \mu_0) - \\ 2(\mu_2 r\hat{M}^{*8} + \mu_1 r\hat{M}^{*4})r\hat{M}^{-2} + \\ r\hat{M}^{*8}\, r\hat{M}^{-4} \end{pmatrix}$$

where $r\hat{M}^*$ is the value of $r\hat{M}$ at which the curves in Fig. 5 are minimized, and the μ_i are defined as shown below:

$$\mu_0 = \frac{(a+3)(a+2)(a+1)a}{(a+b+3)(a+b+2)(a+b+1)(a+b)}$$

$$\mu_1 = \frac{(a+1)a}{(a+b+1)(a+b)}$$

$$\mu_2 = \frac{(a+b-1)(a+b-2)}{(a-1)(a-2)}$$

and

$$\mu_3 = \frac{(a+b-1)(a+b-2)(a+b-3)(a+b-4)}{(a-1)(a-2)(a-3)(a-4)}.$$

It should be noted that the definite integral shown in Equation (29) exists only if the parameter a has a value greater than 4. Because a is a function of rm and CV (Equation (22)), this constraint implies that a maximum admissible CV exists for any given rm, and vice versa:

$$(31)\quad \mathrm{CV}_{max} = \sqrt{\frac{1-\mathrm{rm}}{4+\mathrm{rm}}}$$

and

$$(32)\quad \mathrm{rm}_{max} = \frac{1-4\mathrm{CV}^2}{1+\mathrm{CV}^2}.$$

Differentiating Equation (30) with respect to $r\hat{M}$ and setting the resulting expression equal to zero yields the following three roots:

$$(33)\quad r\hat{M}_{opt} = \begin{pmatrix} \frac{\sqrt{\mu_2 r\hat{M}^{*4} + 2r\hat{M}^{*2} + \mu_1} - \sqrt{\mu_2 r\hat{M}^{*4} - 2r\hat{M}^{*2} + \mu_1}}{2} \\ r\hat{M}^* \\ \frac{\sqrt{\mu_2 r\hat{M}^{*4} + 2r\hat{M}^{*2} + \mu_1} + \sqrt{\mu_2 r\hat{M}^{*4} - 2r\hat{M}^{*2} + \mu_1}}{2} \end{pmatrix}$$

Note that all three roots are independent of μ_0, μ_3, and all three of the k_i. The second root is simply the minimum of the response function, and represents a local maximum of the expected loss function. Expected loss is plotted for the example parameters in Fig. 6.

Because μ_1 and μ_2 are functions of the beta parameters a and b, they can be rewritten in terms of the relative mean and coefficient of variation by substituting Equations (22) and (23), giving

$$(34)\quad \mu_1 = \mathrm{rm}^2(1 + \mathrm{CV}^2)$$

and

$$(35)\quad \mu_2 = \frac{(rm - 1 + 2rm\,CV^2)(rm - 1 + 3rm\,CV^2)}{rm^2\left((rm-1)+(rm+2)CV^2\right)\left((rm-1)+(rm+1)CV^2\right)}.$$

Another convenient substitution is made by defining

$$(36)\quad \rho = \left(\frac{r\hat{M}^*}{rm}\right)^2.$$

Then, for all $\rho \neq 1$, the two minima of the expected loss function can be rewritten in terms of more interpretable parameters as

$$(37)\quad r\hat{M}_{opt} = \left(\frac{rm}{2}\right)\sqrt{\frac{\left(2rm\,CV^2-(1-rm)\right)\left(3rm\,CV^2-(1-rm)\right)\rho^2}{\left((rm+2)CV^2-(1-rm)\right)\left((rm+1)CV^2-(1-rm)\right)}} + 2\rho + 1 + CV^2$$

$$\pm\left(\frac{1-\rho}{|1-\rho|}\right)\left(\frac{rm}{2}\right)\sqrt{\frac{\left(2rm\,CV^2-(1-rm)\right)\left(3rm\,CV^2-(1-rm)\right)\rho^2}{\left((rm+2)CV^2-(1-rm)\right)\left((rm+1)CV^2-(1-rm)\right)}} - 2\rho + 1 + CV^2$$

where the local maximum has been omitted from the solution set.

Equation (37) has been parametrized so that the first value (i.e., the value obtained by choosing the "plus" from the "plus or minus" sign at the beginning of the second line) converges to the certainty-equivalent solution $r\hat{M}_{opt} = rm$ as CV approaches zero. Equation (37) is plotted in terms of rm, CV, and ρ in Fig. 7. In particular, it is interesting to note in Fig. 7b that the optimal choice of $r\hat{M}$ becomes increasingly displaced from $r\hat{M}^*$ as CV increases. Because Y always increases monotonically as $r\hat{M}$ diverges from $r\hat{M}^*$ in either direction, it follows that the optimal catch level *increases* with CV; that is, the optimal catch level increases directly with the level of uncertainty regarding the natural mortality rate. This runs contrary to other decision–theoretic solutions in which increased uncertainty leads to decreased catch levels (e.g., Thompson 1992b). This discrepancy is undoubtedly due at least in part to a difference in the time horizon. Here, the management decision (i.e., catch level) is a short-term one, with loss measured in terms of foregone yield during the coming year. However, if the management decision were a long-term one (e.g., a decision regarding the appropriate SPR level to use in defining a constant-F harvest strategy, or a constant catch to be taken over a large number of years), the relationship between optimal catch level and uncertainty would probably be reversed. In particular, it should be remembered that recruitment is assumed here to remain at the initial equilibrium level during the coming year. For recommendations regarding catches to be taken much further in the future, of course, this assumption would have to be relaxed. A net present value (Clark 1976) or adaptive (Walters 1986) approach would be useful in considering these longer term issues.

Although Fig. 7 is only an illustration based on particular parameter values, it can be shown in fact that this result is completely general (i.e., does not depend on particular parameter values) in the context of the present model. This implies that the catch corresponding to $r\hat{M} = rm$ will never exceed the optimum catch.

Evaluation of Suboptimal Alternatives

In addition to the optimal solution given by Equations (33) and (37), three reasonable, though necessarily suboptimal, alternatives can be examined: (1) setting catch at the level corresponding to the mean of the pdf ($r\hat{M} = rm$), (2) setting catch at the minimum of the yield response function ($r\hat{M} = r\hat{M}^*$), and (3) setting catch at the level corresponding to $\hat{\gamma} = 0$ ($r\hat{M} = 1$). By substituting each of these values into Equation (30), the expected losses associated with each can be computed and compared. For example, the expected loss associated with setting $r\hat{M} = rm$ is always less than that associated with setting $r\hat{M} = r\hat{M}^*$ because rm always falls between $r\hat{M}_{opt}$ and $r\hat{M}^*$ and expected loss is monotone over this range (reaching a maximum at $r\hat{M}^*$).

In contrast, the relationship between the expected loss associated with $r\hat{M} = rm$ and that associated with $r\hat{M} = 1$ is ambiguous. The former will always exceed the latter whenever the following condition holds:

$$(38)\quad \left(\frac{1}{rm}\right)\sqrt{\frac{rm^2-(2\mu_1-1)}{rm^2(2\mu_2-1)-1}} < \rho < \frac{1}{rm}.$$

Satisfaction of this condition may be somewhat rare in cases where rm and ρ are both relatively low. For example, if rm is less than or equal to 1/2, the term on the left-hand side of the first inequality above will always be at least 10/9 for any admissible value of CV. Thus, if rm is less than 1/2 and $r\hat{M}^*$ is no greater than rm (as in the present example), the strategy of setting $r\hat{M} = rm$ will always outperform the strategy of setting $r\hat{M} = 1$.

Finally, the relationship between the expected loss associated with $r\hat{M} = 1$ and that associated with $r\hat{M} = r\hat{M}^*$ is also ambiguous. The former will always exceed the latter whenever the following condition holds:

$$(39)\quad \frac{1-\sqrt{2\left(\mu_2-\mu_1(2\mu_2-1)\right)}}{rm^2(2\mu_2-1)} < \rho < \frac{1+\sqrt{2\left(\mu_2-\mu_1(2\mu_2-1)\right)}}{rm^2(2\mu_2-1)}.$$

Satisfaction of this condition may be fairly common in cases where rm and ρ are both relatively low. For example, the condition specified by the left-hand inequality will always be satisfied for any value of rm less than about 2/3. Of course, transitivity dictates that Conditions (38) and (39) can never be satisfied simultaneously because the expected loss associated with setting $r\hat{M} = rm$ is always less than that associated with setting $r\hat{M} = r\hat{M}^*$.

Conclusions

For the case in which selectivity is allowed to be a nonmonotone function of age, a number of conclusions emerge

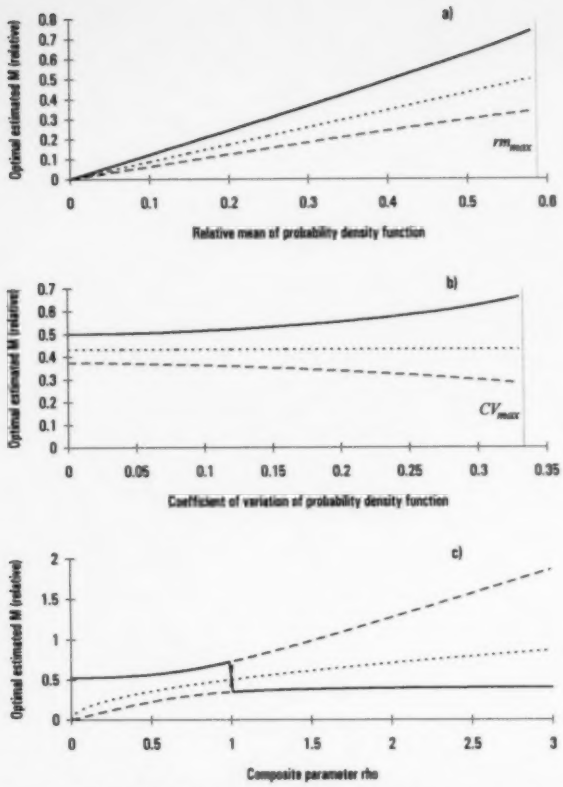


FIG. 7. Behavior of the solution to the model approximation (Equation (33)). Solid curves correspond to the root which returns the certainty-equivalent solution as CV approaches zero, dashed curves correspond to the alternative root, and dotted curves give the local maximum of the objective function.

from the above. It should be stressed that all of these are contingent on the assumptions employed. In particular, because the target SPR level is assumed to be fixed a priori, it should be remembered that any of the methods suggested here will be only as good as the target SPR level supplied. Given these caveats, the following are the central conclusions of this study.

(1) Even with auxiliary information, it may be impossible in a typical catch-age analysis to estimate both M and the full set of parameters governing the selectivity schedule (Equation (15); Fig. 2a).

2) In contrast to what appears to be emerging as the conventional wisdom (e.g., as cited by Hilden 1988), a 1-yr forecast of the catch corresponding to an intended harvest strategy such as a fixed equilibrium level of SPR can vary dramatically with either M or a selectivity parameter (Equation (19); Figs. 2d and 5).

(3) The profile of catch against M or a selectivity parameter may contain a minimum, which could correspond to an upper bound on allowable harvest if the prescribed level of SPR defines something like a maximum sustainable F (Figs. 2d and 5).

(4) If the prescribed level of SPR instead incorporates a reasonable margin for error, then use of the quadratic loss function suggested here (which always maps the minimum of the harvest response function into a local maximum of the expected loss curve) leads to an optimal catch level which typically exceeds the minimum of the harvest response function and which typically increases as the level of uncertainty intensifies and values of M displaced from the mean become increasingly plausible (Equation (37), Fig. 7).

(5) Fixing M at its expected value (i.e., at the mean of its probability density function) should not cause the optimal catch level to be exceeded, and should result in an expected loss less than that associated with the minimum point of the response function (Equation (37), Fig. 7).

(6) Constraining selectivity to be asymptotic (so as to allow internal estimation of M) should result in an expected loss less than that associated with fixing M at its expected value only in certain cases (Equation (38)), and may even give poorer results than choosing the minimum point of the response function (Equation (39)).

Acknowledgments

I would like to thank William G. Clark, James A. Ianelli, Richard D. Methot, Benjamin J. Turnock, and an anonymous referee for helpful comments.

References

AGGER, P., I. BOETIUS, AND M. LASSEN. 1973. Error in the virtual population analysis: the effect of uncertainties in the natural mortality coefficient. J. Cons. int. Explor. Mer 35: 93.

BENCE, J.R., A. GORDOA, AND J.E. HIGHTOWER. 1993. Influence of age-selective surveys on the reliability of stock synthesis assessments. Can. J. Fish. Aquat. Sci. 50: 827–840.

CLARK, C.W. 1976. Mathematical bioeconomics: the optimal management of renewable resources. Wiley, New York, N.Y. 352 p.

CLARK, W.G. 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48: 734–750.

DEGROOT, M.H. 1970. Optimal statistical decisions. McGraw-Hill, New York, N.Y. 489 p.

DERISO, R.B., P.R. NEAL, AND T.J. QUINN II. 1989. Further aspects of catch-age analysis with auxiliary information, p. 127–135. *In* R.J. Beamish and G. A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.

DERISO, R.B., T.J. QUINN II, AND P.R. NEAL. 1985. Catch-age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42: 185–824.

DOUBLEDAY, W.G. 1976. A least squares approach to analyzing catch at age data. Int. Comm. Northwest Atl. Fish. Res. Bull 12: 69–81.

FOURNIER, D.A. 1983. An analysis of the Hecate Strait Pacific cod fishery using an age-structured model incorporating density-dependent effects. Can. J. Fish. Aquat. Sci. 40: 1233–1243.

FOURNIER, D.A., AND C. ARCHIBALD. 1982. A general theory for analyzing catch at age data. Can. J. Fish. Aquat. Sci. 39: 1195–1207.

GOODYEAR, C.P. 1977. Assessing the impact of power plant mortality on the compensatory reserve of fish populations, p. 186–195. *In* W. Van Winkle [ed.] Proceedings of the Conference on Assessing the Effects of Power Plant Induced Mortality on Fish Populations. Pergamon Press, New York, N.Y.

GOODYEAR, C.P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use, p. 67–81. *In* S.J. Smith, J.J. Hunt, and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

HILDEN, M. 1988. Errors of perception in stock and recruitment studies due to wrong choices of natural mortality rate in virtual population analysis. J. Cons. int. Explor. Mer 44: 123–134.

HOGG, R.V., AND A.T. CRAIG. 1970. Introduction to mathematical statistics (3rd ed.). Macmillan, New York, N.Y. 415 p.

HULME, H.R., R.J.H. BEVERTON, AND S.J. HOLT. 1947. Population studies in fisheries biology. Nature (Lond.) 159: 714–715.

LAPOINTE, M.F., R.M. PETERMAN, AND A.D. MacCALL. 1989. Trends in fishing mortality rate along with errors in natural mortality rate can cause spurious time trends in fish stock abundances estimated by virtual population analysis (VPA). Can. J. Fish. Aquat. Sci. 46: 2129–2139.

MACE, P.M., AND M.P. SISSENWINE. 1993. How much spawning per recruit is enough? p. 101–108. *In* S.J. Smith, J.J. Hunt, and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

METHOT, R.D. 1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data, p. 259–277. *In* L.-L. Low [ed.] Proceedings of the Symposium on Application of Stock Assessment Techniques to Gadids. Int. North Pac. Fish. Comm. Bull. 50.

PALOHEIMO, J.E. 1980. Estimation of mortality rates. Trans. Am. Fish. Soc. 109: 378–386.

POPE, J.G. 1983. Analogies to the status quo TACs: their nature and variance, p. 99–113. *In* W.G. Doubleday and D. Rivard [ed.] Sampling commercial catches of marine fish and invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 66.

SAMPSON, D.B. 1987. Variance estimators for virtual population analysis. J. Cons. int. Explor. Mer 43: 149–158.

SAMPSON, D.B. 1993. The assumption of constant selectivity and the stock assessment for widow rockfish, *Sebastes entomelas*. Fish. Bull. (U.S.) 91: 676–689.

SIMS, S.E. 1984. An analysis of the effect of errors in the natural mortality rate on stock-size estimates using virtual population analysis (cohort analysis). J. Cons. int. Explor. Mer 41: 149–153.

THOMPSON, G.G. 1992a. Management advice from a simple dynamic pool model. Fish. Bull. (U.S.) 90: 552–560.

THOMPSON, G.G. 1992b. A Bayesian approach to management advice when stock–recruitment parameters are uncertain. Fish. Bull. (U.S.) 90: 561–573.

THOMPSON, G.G. 1993. A proposal for a threshold stock size and maximum fishing mortality rate, p. 303–320. *In* S.J. Smith, J.J. Hunt, and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

THOMPSON, G.G., AND R.G. BAKKALA. 1990. Assessment of the eastern Bering Sea Pacific cod stock using a catch-at-age model and trawl survey data, p. 215–236. *In* L.-L. Low [ed.] Proceedings of the Symposium on Application of Stock Assessment Techniques to Gadids. Int. N. Pac. Fish. Comm. Bull. 50.

ULLTANG, O. 1977. Sources of errors in and limitations of virtual population analysis (cohort analysis). J. Cons. int. Explor. Mer 37: 249–260.

WALTERS, C.J. 1986. Adaptive management of renewable resources. MacMillan, New York, N.Y. 374 p.

Appendix A: Proof that the Double Logistic Function Contains the Exponential-Logistic Function as a Special Case

The double logistic function takes its name from the fact that it can be written as the product of two logistic functions. Define two such functions L_1 and L_2 as follows:

$$\text{(A1)}\quad L_1(x) = \frac{1}{1 + e^{\alpha(\beta - x)}}$$

and

$$\text{(A2)}\quad L_2(x) = \frac{1}{1 + e^{-\alpha\gamma(\phi - x)}}$$

where α, β, γ, and ϕ are constants. The inflection points of L_1 and L_2 occur at $x = \beta$ and $x = \phi$, respectively. The slope of L_1 at $x = \beta$ is $\alpha/4$. The slope of L_2 at $x = \phi$ is equal to $-\gamma$ times the slope of L_1 at $x = \beta$.

Let x_p represent the value of x at which the product of L_1 and L_2 is maximized. Then, define

$$\text{(A3)}\quad \lambda = (1 + e^{\alpha(\beta - x_p)})(1 + e^{-\alpha\gamma(\phi - x_p)})$$

in which case the scaled form of the double logistic function can be written

$$\text{(A4)}\quad S(x) = \frac{\lambda}{(1 + e^{\alpha(\beta - x)})(1 + e^{-\alpha\gamma(\phi - x)})}$$

Note that this relationship can be rewritten as

$$\text{(A5)}\quad S(x) = \left(\frac{\lambda}{(1 + e^{\alpha(\beta - x)})(1 + e^{-\alpha\gamma(\phi - x)})}\right)\left(\frac{e^{\alpha\gamma(\phi - x)}}{e^{\alpha\gamma(\phi - x)}}\right)$$

$$= \frac{\lambda e^{\alpha\gamma(\phi - x)}}{(1 + e^{\alpha(\beta - x)})e^{\alpha\gamma(\phi - x)} + (1 + e^{\alpha(\beta - x)})}.$$

The exponential–logistic function is described by Equation (1) in the main text, with a peak occurring at the value x_p shown in Equation (2). If the exponential–logistic function is contained as a special case of the double logistic function, then it should be possible to substitute the value of x_p from Equation (2) into Equation (A3) in order to define a special case $\hat{\lambda}$:

$$\text{(A6)}\quad \hat{\lambda} = \left(\frac{1}{1 - \gamma}\right)\left[1 + \left(\frac{1 - \gamma}{\gamma}\right)^{\gamma} e^{\alpha\gamma(\beta - \phi)}\right].$$

This value can in turn be substituted into Equation (A5) to define a special case $\hat{S}(x)$:

$$\text{(A7)}\quad \hat{S}(x) = \frac{\left(\frac{1}{1 - \gamma}\right)e^{\alpha\gamma(\phi - x)} + \left(\frac{1}{1 - \gamma}\right)\left(\frac{1 - \gamma}{\gamma}\right)^{\gamma} e^{\alpha\gamma(\beta - x)}}{(1 + e^{\alpha(\beta - x)})e^{\alpha\gamma(\phi - x)} + (1 + e^{\alpha(\beta - x)})}.$$

Note that as ϕ approaches negative infinity, the left-hand terms in both the numerator and denominator of Equation (A7) go to zero, reducing the equation exactly to the exponential–logistic (Equation (1) in the main text). Therefore, the exponential–logistic function is a special case of the double logistic function, obtained in the limit as the inflection point of L_2 approaches negative infinity.

Appendix B: Derivation of Annual Yield under Fishing Mortality Rate F from a Stock at Initial Equilibrium under Fishing Mortality Rate F_0

Numbers-at-age $n(x)$ under an initial equilibrium defined by a fishing mortality rate F_0 can be written

$$\text{(B1)}\quad n(x) = Re^{-(M + F_0)(x - x_r)}$$

where R is the recruitment rate (in numbers) and M is the natural mortality rate.

The linear growth schedule used by Thompson (1992a) can be written

$$\text{(B2)}\quad w(x) = w_r(1 + \delta(x - x_r))$$

where $w(x)$ represents weight at age x, x_r is the age of knife-edge recruitment to the commercial fishery, w_r is weight at age x_r, and δ is the reciprocal of the difference between age x_r and the age intercept of the weight–age relationship.

Yield-at-age $y(x)$ during the coming year from all fish currently in the stock is then

$$\text{(B3)}\quad y(x) = Fn(x)\int_x^{x+1} w(t)s^{t-a}\,dt$$

$$= Fn(x)\left(w_r\delta\int_x^{x+1} ts^{t-x}\,dt + w(0)\int_x^{x+1} s^{t-x}\,dt\right)$$

$$= n(x)\left[uw(x) + (u - Fs)w_r\left(\frac{\delta}{M + F}\right)\right]$$

where the survival rate is given by $s = e^{-(M+F)}$ and Baranov's exploitation rate is given by $u = F(1 - s)/(M + F)$.

Integrating across age x gives the total yield over the coming year from fish which are already in the stock:

$$\text{(B4)}\quad Y_1 = \int_{x_r}^{\infty} y(x)dx$$

$$= \left(\frac{Rw_r}{M+F}\right)\left[u\left(\frac{\delta}{M+F}+\frac{\delta}{M+F_0}+1\right)-Fs\left(\frac{\delta}{M+F}\right)\right].$$

By definition, Y_1 excludes yield from fish which recruit during the year. The yield over the coming year from fish which recruit during the year is given by

$$\text{(B5)}\quad Y_2 = FR\int_0^1\int_t^1 w(x_r+x-t)s^{x-t}dxdt$$

$$= FRw_r\left[s\left(\frac{1+\delta}{(M+F)^2}+\frac{2\delta}{(M+F)^3}\right)\right.$$

$$\left.+\left(\frac{1}{M+F}-\frac{1-\delta}{(M+F)^2}-\frac{2\delta}{(M+F)^3}\right)\right].$$

The sum of Y_1 and Y_2 then gives total yield over the coming year, both from those fish which are already in the stock and those which will recruit during the year:

$$\text{(B6)}\quad Y = Rw_r\left(\left(\frac{F}{M+F}\right)\left[\left(\frac{\delta}{M+F}+1\right)\right.\right.$$

$$\left.+s\left(\frac{\delta}{M+F}-\frac{\delta}{M+F_0}\right)\right]$$

$$+u\left[\left(\frac{1}{M+F_0}\right)\left(\frac{\delta}{M+F}+\frac{\delta}{M+F_0}+1\right)\right.$$

$$\left.\left.-\left(\frac{1}{M+F}\right)\left(\frac{2\delta}{M+F}+1\right)\right]\right).$$

Modeling Predator–Prey Dynamics in a Fluctuating Environment

Jeremy S. Collie and Paul D. Spencer

Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA

Collie, J.S., and P.D. Spencer. 1994. Modeling predator–prey dynamics in a fluctuating environment. Can. J. Fish. Aquat. Sci. 51: 2665–2672.

Large fluctuations in the abundance of marine fish are revealed in scale deposits from before the twentieth century and are thought to be environmentally induced. We investigated how a fluctuating environment and predation may combine to cause abrupt shifts in fish abundance on decadal time scales. For example, the biomass of Pacific herring (*Clupea pallasi*) off Vancouver Island appears to be negatively related to sea surface temperature (SST) and the abundance of its predator, Pacific hake (*Merluccius productus*). We used first-order differential equations to develop a two-species, predator–prey model forced with stochastic variability. A nonlinear, predator functional response potentially gives rise to multiple equilibrium abundance levels. Environmental variability was simulated as "red noise" (variance is a decreasing function of frequency) with a spectrum derived from SST data. Stochastic variations caused the predator–prey abundances to shift between high and low equilibrium levels. Fishing the prey population can precipitate collapses to the low equilibrium level and prolong the time to recovery. When run with actual catches and SST anomalies from 1951 to 1988, the model simulated prey abundances with a pattern similar to the observed herring biomass.

Des dépôts d'écailles remontant avant le début du vingtième siècle ont révélé de grandes fluctuations d'abondance chez les poissons marins, fluctuations qui sembleraient écogéniques. Nous étudions comment un environnement variable et la prédation peuvent se conjuguer et provoquer des variations soudaines de l'abondance du poisson à l'échelle des décennies. Par exemple, la biomasse du hareng du Pacifique (*Clupea pallasi*), au large de l'île de Vancouver, semble être liée négativement à la température de surface de la mer et à l'abondance de son prédateur, le merlu du Pacifique (*Merluccius productus*). Au moyen d'équations différentielles de premier ordre, nous avons élaboré un modèle prédateur–proie à deux espèces reposant sur la variabilité aléatoire. L'obtention d'une fonction prédateur non linéaire peut éventuellement donner lieu à plusieurs niveaux d'abondance en équilibre. La variabilité environnementale a été simulé sous forme de « bruit rouge » (la variance est une fonction décroissante de la fréquence) avec un spectre obtenu à partir des données sur la température de surface de la mer. Des variations aléatoires sont à l'origine du passage de l'abondance prédateur–proie d'un niveau d'équilibre supérieur à un niveau inférieur. L'exploitation de la population proie peut accélérer les effondrements au niveau d'équilibre supérieur et prolonger la durée de rétablissement. Lorsque le modèle est exécuté avec les prises réelles et les anomalies des températures de la surface de la mer de 1951 à 1988, il simule l'abondance des proies avec un profil similaire à la biomasse observée.

Received February 9, 1994
Accepted October 4, 1994
(J12269)

Reçu le 9 février 1994
Accepté le 4 octobre 1994

Understanding the causes of recruitment variability has been a major concern of fisheries scientists ever since Johan Hjort discovered that fluctuations in the abundance of "the great fisheries of Northern Europe" result largely from interannual variability in recruitment (Hjort 1914). Nevertheless, recruitment variability of most fish stocks remains unexplained. If needed, an adequate assessment program can provide fisheries managers the information necessary to respond to interannual changes in abundance (Walters and Collie 1988); however, the explanation of recruitment patterns would be a valuable contribution to fisheries science.

Recently, as longer data sets have become available and concern about potential long-term effects of climate change has increased, fisheries scientists have turned to variability in fish populations occurring on decadal time scales (Kawasaki et al. 1991). Regime shifts are particularly apparent in the North Pacific, both in the physical environment and in patterns of fish recruitment (Hollowed and Wooster 1992). Causes of these regime shifts are uncertain, but some combination of fishing pressure and environmental variability is likely; environmental variability may manifest itself through trophic interactions (Skud 1982). Large-amplitude regime shifts hinder efforts to obtain sustainable harvests from fisheries, as standard analyses of acceptable harvest and overfishing levels are frustrated by apparent shifts in productivity. Presently, there is very limited capability to predict when, if ever, regime shifts will reverse.

In this study, we describe an approach for introducing realistic ocean forcing and trophic interactions into population dynamics models. In the first part, we review examples of long-term fluctuations in Pacific hake (*Merluccius productus*) and Pacific herring (*Clupea pallasi*). In the second part, we develop a predator–prey model, based on Steele and Henderson (1981, 1994), and demonstrate how environmental variability can cause abundance shifts. Finally, we apply the model to the Pacific hake and Pacific herring stocks off the west coast of Vancouver Island, British Columbia.

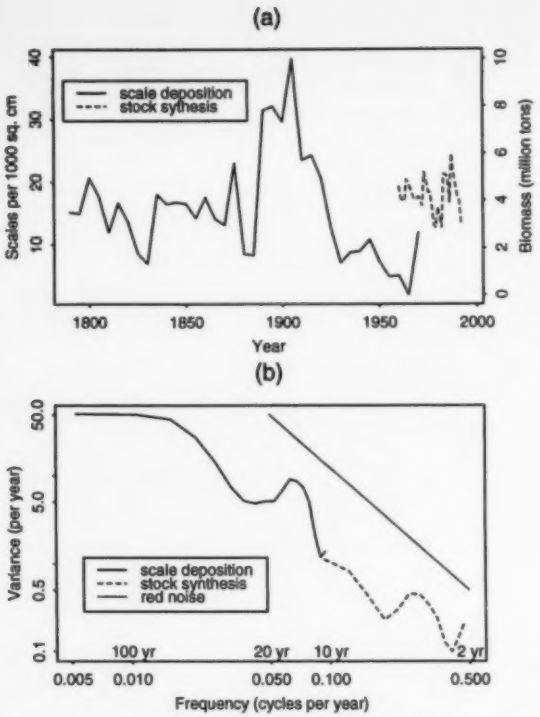


FIG. 1. (a) Time series of Pacific hake abundance. Scale-deposition data were calculated from Smith (1978); recent biomass estimates are from a stock synthesis population model (Dorn and Methot 1993). (b) Combined spectrum of the hake time series. The spectra were smoothed with a moving average of length 5. The scale-deposition spectrum was divided by 20 to align it with the stock-synthesis spectrum. The slope for red noise, -2, is shown by the dotted line.

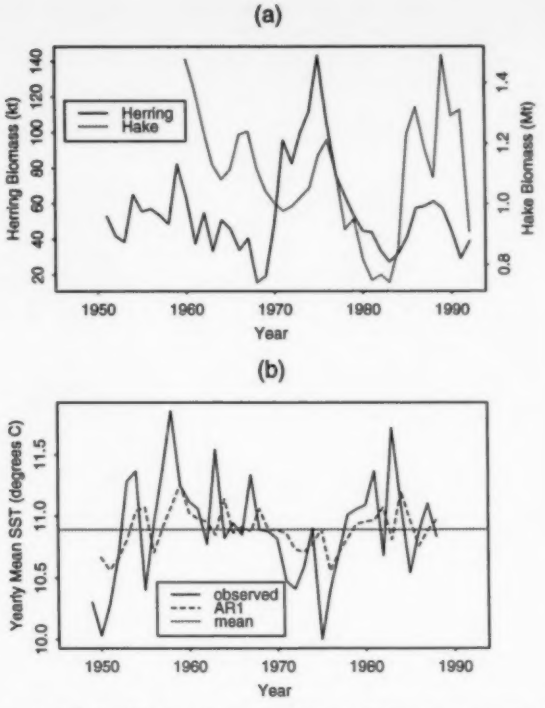


FIG. 2. (a) Pacific herring abundance off the west coast of Vancouver Island (from Schweigert et al. 1993) and Pacific hake abundance in Canadian waters (M. Dorn, Alaska Fisheries Science Center, personal communication). (b) Sea surface temperature (SST) off the west coast of Vancouver Island. The data are from the 2° × 2° COADS square centered at 127°W, 49°N. A first-order autoregressive model (AR1) is the optimal auto-regressive model fit to these data.

Long-term Fluctuations in Pacific Hake and Pacific Herring Abundance

For most commercially exploited fish species, catch records alone are too short to resolve interdecadal fluctuations. Anaerobic, varved sediment cores collected in the Santa Barbara Basin provide measures of relative abundance of fish scales for the past 1700-yr period (Baumgartner et al. 1992). Pacific hake is one species for which the age-structured stock assessment (Dorn and Methot 1993) can be combined with scale-deposition estimates of abundance, reported by Smith (1978). However, intercalibration of the two time series is uncertain because only three of the scale-depostion estimates overlap the recent stock assessment. Also, uncertainty in the target strength used to estimate biomass from hydroacoustic surveys creates uncertainty in the stock-synthesis estimates (Dorn and Methot 1993). The scale-depostion data illustrate that the longer the time frame considered, the greater the variability (Fig. 1a) and suggest 50- to 60-yr periodicity. Variance at these periods has been documented in scale-deposition rates of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) (Baumgartner et al. 1992) and in time series of physical variables measured off California (Ware and Thompson 1991).

The contribution of each frequency (period) to the total variance in abundance can be examined with spectral analysis. We constructed a composite spectrum of Pacific hake abundance with the combined scale-deposition and stock-assessment time series. Each series was detrended prior to calculating the spectra, and the periodogram was smoothed with a modified Daniell window of length 5 to reduce variability (StatSci 1991). We calibrated the scale-deposition data to align the spectra in Fig. 1b; the relative scaling is approximately as shown in Fig. 1a. Thus the two time series are calibrated in the frequency domain (Fig. 1b) and not the time domain (Fig. 1a). This scaling affects the vertical alignment of the spectra but not their slopes because variance is plotted on a log scale.

The smoothed spectrum shows the amount of variance occurring over a range of frequencies with corresponding periods from 2 to 200 yr (Fig. 1b). There is a continuum of variance, with most of the power at long time scales. Peaks in the spectrum correspond to periods of 4 and 14 yr. The 4-yr periodicity corresponds to the average interval between strong hake year-classes (Dorn and Methot 1993); the peak at 14 yr is unexplained. Neither peak differs significantly from the monotonically decreasing trend. This pattern of decreasing variance with increasing frequency is referred to as red noise (in contrast with white noise, in

which variance is constant with frequency). The slope of the descending part of the spectrum is approximately -2 on the logarithmic scale, which is the slope for red noise. Red spectra have previously been observed in marine communities (Steele 1985; Aebischer et al. 1990); Pacific hake provides a good example spanning a wide range of frequencies. This is the type of variability pattern fisheries models should capture.

Pacific hake is a seasonal predator of the herring stock off the west coast of Vancouver Island, British Columbia. Herring, like other clupeoid fishes, exhibits large-amplitude fluctuations in abundance on decadal time scales (Skud 1982; Southward et al. 1988; Collie and Spencer 1993). By the late 1960s, the herring stock off the west coast of Vancouver Island had been reduced to very low levels, following several years of high fishing mortality; the fishery was closed from 1968 to 1971 (Schweigert et al. 1993). Thereafter, the herring stock peaked in abundance in the early 1970s and then declined to previous levels (Fig. 2a). The abundance of hake in Canadian waters declined during the 1960s and 1970s and increased in the 1980s. The low levels of herring biomass in the 1960s and 1980s could be partly explained by high levels of hake predation during these periods.

Haist et al. (1993) attributed the decline in British Columbia herring stocks in the late 1960s to a series of poor year-classes in conjunction with intensive fisheries and increased natural mortality. The assumption of increasing natural mortality at low herring stock abundance provided a significantly better fit to the catch-at-age data fisheries data than a constant natural mortality rate. This evidence of depensatory natural mortality is consistent with the hypothesis that the predator community consumes a higher proportion of the herring stock as stock biomass decreases. Recruitment of the Hecate Strait herring stock appears to be negatively related to Pacific cod (*Gadus macrocephalus*) biomass (Walters et al. 1986). The herring mortality rate due to cod predation, estimated with a modified Ricker model, agreed with stomach-content data.

Ware and McFarlane (1986) estimated the predatory impact of hake on the west coast of Vancouver Island herring stock. The two principal prey of hake are euphausids and herring, with herring contributing up to 59% of the diet by volume (Tanasichuk et al. 1991). A linear regression model revealed that herring year-class strength was negatively correlated with hake ration and sea surface temperature (SST), indicating that recruitment depends on both predator abundance and environmental conditions. A possible explanation of this result is that the northern migration of hake is temperature dependent (Ware and McFarlane 1986). In warm years, the hake migrate further north and spend more time feeding in Canadian waters, where the herring stock summers (Smith et al. 1990). Thus the hake–herring example is consistent with a predator–prey model in which the predation rate is temperature dependent.

Low SST off the west coast of Vancouver Island in the early 1970s (Fig. 2b) coincided with the peak in herring abundance (Fig. 2a), suggesting that the model of temperature-dependant predation is plausible. These temperature data are from the Comprehensive Ocean–Atmosphere Data Set (COADS, Woodruff et al. 1987). According to the Akaike Information Criterion, a first-order autoregressive (AR1) model is the optimal autoregressive model for the annual mean SST data. This result justifies the use of the autoregressive model to simulate environmental variability in population models. In the model described below, we use an autoregressive model with random variability and also the actual SST data to introduce variability in the predation rate. The SST spectrum (not shown) is a decreasing function of frequency, similar to the hake spectrum. There is a peak at periods of about 4 yr, corresponding roughly with the frequency of El Niño/Southern Oscillation events.

Predator–Prey Model

This work builds on a predator–prey model developed by Steele and Henderson (1981) to describe the dynamics of phytoplankton and herbivorous zooplankton. Steele and Henderson (1994) suggested that similar models could explain the fluctuations of marine fish populations. The predator–prey model is a pair of coupled, first-order differential equations describing the rate of change of prey (P) and predator (H) biomass:

$$(1)\quad \frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right) - \frac{CHP^2}{(A^2 + P^2)} - FP$$

$$(2)\quad \frac{dH}{dt} = \frac{gHP^2}{(A^2 + P^2)} - DH^2.$$

The prey equation is based on the logistic model with intrinsic growth rate, r, and carrying capacity, K. The predator is assumed to have a Type III functional response with consumption rate, C, and prey threshold level, A. Predator production depends on prey abundance, with a growth rate (g) and a quadratic mortality term (D). Fishery yield is assumed proportional to prey abundance with fishing mortality rate, F. In this application, fishing occurs only on the prey population, although the predator could potentially be harvested as well.

Equilibrium Analysis

The equilibrium properties of the predator–prey equations can be better understood by transforming the variables such that, $X = P/A$ is prey abundance, $Y = CH/A$ is predator abundance, $k = K/A$ is prey carrying capacity, and $d = rAD/gC$ is the predator mortality rate.

The rescaled prey–predator equations are

$$(3)\quad \frac{dX}{dt} = rX\left(1 - \frac{X}{k}\right) - \frac{YX^2}{(1 + X^2)} - FX$$

$$(4)\quad \frac{dY}{dt} = gY\left(\frac{X^2}{(1 + X^2)} - \frac{dY}{r}\right).$$

Rescaling leaves only four free parameters, plus F. The predator equation is like the standard logistic, except the growth rate, instead of being constant, depends on prey abundance.

The equilibrium analysis proceeds by examining the species isoclines, where the rate of change of a species is zero (Fig. 3). The prey isocline is dome-shaped and bends upward near the origin; the predator isocline is sigmoidal. Where the isoclines intersect, the two species are at equilibrium. For certain parameter combinations, there is an upper and lower stable equilibrium separated by an unstable equilibrium level. Changes in model parameters shift the isoclines and

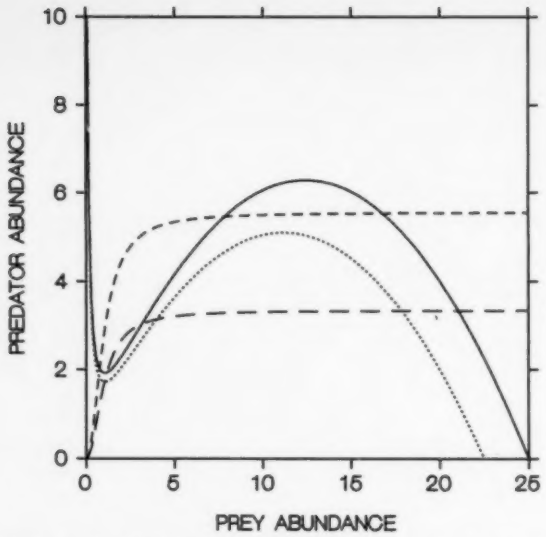


FIG. 3. Species isoclines for the rescaled model, with $r = 1$, k = 25, and $g = 0.5$. The solid line is the prey isocline without fishing and the dotted line is the prey isocline with $F = 0.1$. The broken line is the predator isocline with $d = 0.3$ and the dashed line is the predator isocline with $d = 0.18$. Equilibrium points occur where the isoclines intersect, with the outer equilibrium points being stable and the middle equilibrium point being unstable.

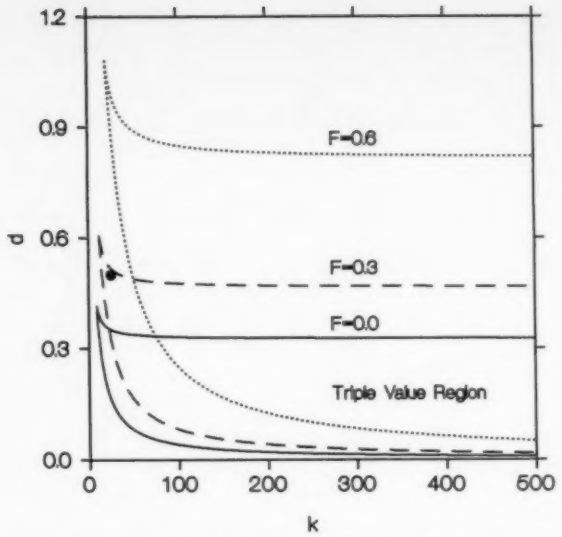


FIG. 4. Combinations of the k and d parameters for which there exist triple-value solutions for the rescaled model, with $r = 1$ and $F = 0.0$ (solid), 0.3 (broken), and 0.6 (dotted). The combination of $k = 25$ and $d = 0.5$ (solid point) is at the high-prey equilibrium with $F = 0.0$, in the triple value region with $F = 0.3$, and at the low-prey equilibrium with $F = 0.6$.

equilibrium points. For example, a decrease in predator mortality (d) increases predator production and shifts the predator isocline upwards. If the predator isocline is shifted far enough, the system will have only the low, stable equilibrium point. Thus, when variability is introduced to the model, the system can alternate between the stable equilibria. The small difference in equilibrium predator levels and large difference in prey equilibrium levels explain how gradual changes in predation can be amplified to abrupt changes in prey abundance. Fishing mortality on the prey reduces its equilibrium abundance, eventually to a level at which only the low equilibrium level remains (Fig. 3).

For given values of r and F, three equilibria exist for a combinations of k and d values (Fig. 4); we call this the triple-value region. For higher levels of mortality on the predator (d), there is a single high-prey equilibrium. For low predator mortality, there is a single low-prey equilibrium. Thus, variability in d can cause the populations to flip from one equilibrium level, through the triple-value region, to the other equilibrium. For each level of fishing mortality, there is a different triple-value region. Increased fishing increases the combinations of k and d that result in the single, low equilibrium, thus shifting the location of the triple-value region upward in Fig. 4. For example, with the combination of k and d parameters indicated by the solid point in Fig. 4, the prey population would be at the upper equilibrium level with $F = 0$, in the triple-value region with $F = 0.3$, and at the low equilibrium level with $F = 0.6$.

The shift of equilibrium prey abundance with increasing F results in two equilibrium yield curves for the prey population: one for high equilibrium levels and one for low (Fig. 5). As fishing mortality is increased from zero, equilibrium yield increases and remains high up to a break point ($F = 0.44$) at which the population flips to the lower equilibrium level. In a purely deterministic model, the only way to return to the upper equilibrium curve is to reduce fishing mortality below the lower break point ($F = 0.28$). In a stochastic model, the prey population could flip back to the upper equilibrium level with a favorable environmental change.

Stochastic Simulations

We introduced environmental variability into the full model by forcing the D parameter with environmental variability such that

$$D_t = D_0 + \nu_t \quad (5)$$

where D_0 is the mean value of D. The environmental variability, ν_t, was computed as

$$\nu_t = \rho\nu_{t-1} + \mu\epsilon_t \quad (6)$$

where ρ is the first-order autocorrelation coefficient and ϵ is a normally distributed random variable with zero mean and unit variance, scaled by μ. This equation was used by Steele and Henderson (1994), and its use here is justified by providing the best fit to the SST data off the west coast of Vancouver Island (Fig. 2b). Equation (6) can give rise to a variety of patterns of variability: $\rho = 0$ gives white noise, $\rho = 1$ produces an unbounded random walk (red noise), and $0 < \rho < 1$ has bounded variance as $t \to \infty$.

A stochastic version of the model was used to simulate the predator–prey dynamics of the herring and hake. The biomass-specific intrinsic growth rate of herring (r) was estimated by converting a value of r obtained with a Ricker stock–recruitment curve into biomass units, which yielded an initial estimate of 0.9. This estimate was increased to 1.1 to compensate for explicitly including the mortality from

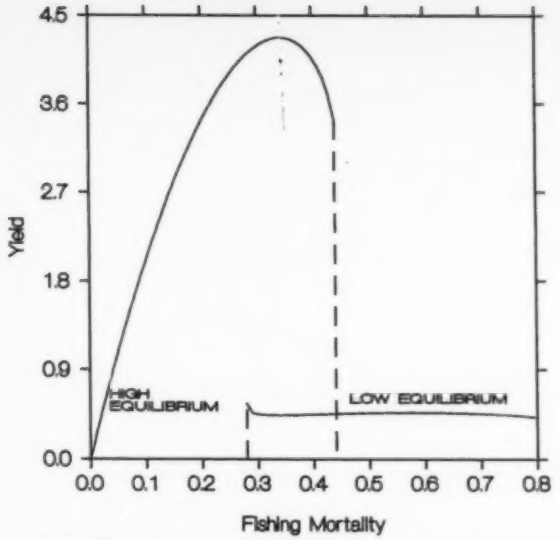


FIG. 5. Equilibrium prey yield (in arbitrary units) as a function of fishing mortality for the rescaled model, with $r = 1$, $k = 25$, and $d = 0.5$. These parameter values correspond to the solid point in Fig. 4.

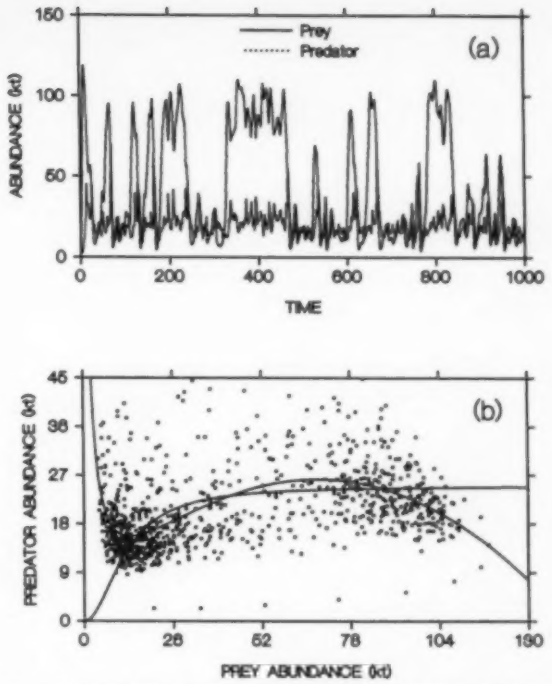


FIG. 6. (a) Simulated predator (Pacific hake) and prey (Pacific herring) abundance over 1000 time steps for the full model, with $r = 1.1$, $K = 216$, $C = 1$, $A = 12$, $F = 0.38$, $g = 0.5$, $D_0 = 0.02$, $\rho = 0.4$, and $\mu = 0.008$. (b) Time series of predator and prey abundance in the predator–prey phase space.

predation in our modified logistic model. The biomass-specific growth rate of hake (g) was inferred by analogy from the growth rate of other gadoid species. For example, the biomass-specific growth rate of Bering Sea pollock was estimated as 0.6 (Quinn and Collie 1990); we chose a value of 0.5 for the hake. Herring fishing mortality was set to the mean of observed mortalities from 1951 to 1992 (0.38). The autocorrelation coefficient ($\rho = 0.4$) was estimated from the SST data off Vancouver Island. In the frequency domain, the simulated environmental variability has a reddish spectrum similar to the spectrum of the observed SST data. The remaining parameters were tuned such that the prey population would fluctuate with the same amplitude and frequency as the observed herring population. Equations (1) and (2) were integrated numerically with the Runge–Kutta method. The value of D was varied each year according to Equations (5) and (6).

The parameters used for the simulation represent a system initially in the triple-value region and alternating between the high and low equilibrium points on time scales of 10–100 yr (Fig. 6a). The remaining parameters were $K = 216$, $C = 1$, $A = 12$, $D_0 = 0.02$, and $\mu = 0.008$. The prey fluctuated much more than the predator, as small changes in predator abundance caused busts and booms in the prey population. By plotting predator abundance against prey abundance at each time step, we can observe dynamics in the predator–prey phase space (Fig. 6b). Most of the 1000 realizations tended to cluster around the two stable equilibria, but there was considerable variability. Predator outbreaks caused the prey to shift to the low equilibrium level; low predator abundance allowed the prey to increase to the upper stable equilibrium. Even though the fluctuations in population abundance were environmentally driven, the prey population was still very sensitive to fishing pressure. At $F = 0$ the prey population remained at the upper equilibrium level, at $F = 0.4$ the population flipped between the equilibrium levels, and at $F > 0.45$, it stayed at the low equilibrium (Fig. 7).

To test whether the predator–prey model is consistent with the actual hake–herring dynamics, we resimulated the population abundances with the actual herring fishing mortality rate (F_t) and SST anomaly in each year from 1951 to 1988 (Fig. 8). Initial prey biomass, P_0, was set to the value observed in 1951. The first simulation used the same set of population parameters as for the stochastic simulations (Fig. 6). The simulated herring biomass decreased sharply in 1959 in response to high fishing mortality ($F = 1.8$) and positive SST anomalies (Fig. 2b). The herring population increased in the early 1970s in response to the closure of the fishery from 1968 to 1971 and negative SST anomalies (less predation). After 1975, the observed and predicted trajectories diverged. Relatively low levels of fishing mortality allowed the simulated population to persist at high abundance. The observed decline to lower abundance levels cannot be explained by fishing patterns alone. The average fishing mortality rate was 0.64 before the fishery closure and 0.24 afterward. We hypothesize that lower fishing mortality after 1975 must be balanced by increased predation mortality.

In the second simulation, we increased the consumption rate, C, and the SST scaling factor to increase predation mortality. Simulated biomass did decrease in the 1980s but with a lag compared with the observed data (Fig. 8). The second parameter set lies outside the triple-value region, such that only the single low-prey equilibrium exists with

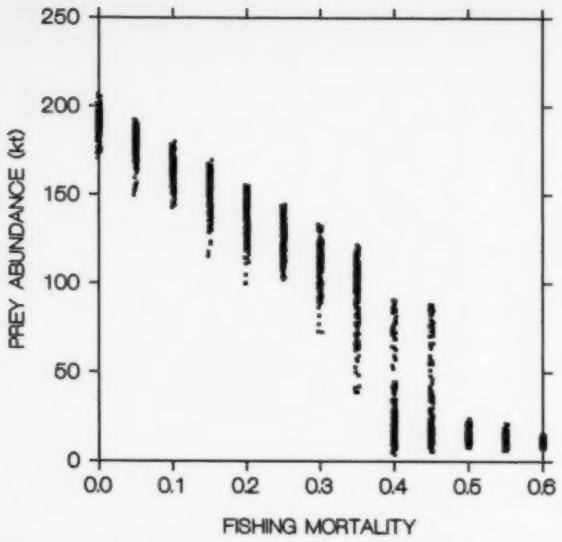


FIG. 7. Simulated prey (Pacific herring) abundance as a function of fishing mortality for the full model, with $r = 1.1$, $K = 216$, $C = 1$, $A = 12$, $g = 0.5$, $D_o = 0.02$, $\rho = 0.4$, and $\mu = 0.008$. Abundance over 200 time intervals is plotted for each level of F.

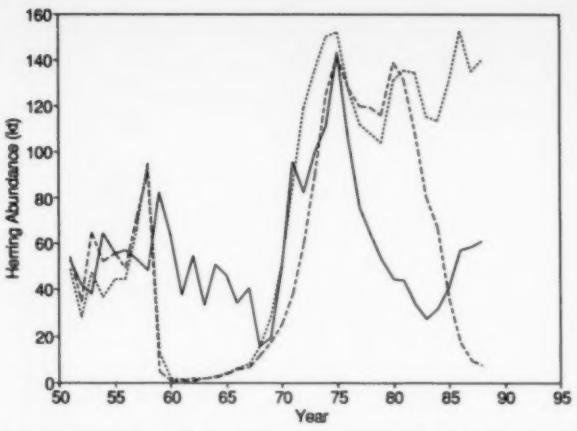


FIG. 8. Comparison of the full predator–prey model with observed biomass of Pacific herring (solid line) when observed fishing mortalities and temperature anomalies are used. The dotted line is model output with the parameters used for the simulation in Fig. 6 ($r = 1.1$, $K = 216$, $C = 1$, $A = 12$, $g = 0.5$, $D_o = 0.02$); this parameter combination provides a solution in the triple-value region. The broken line is model output with $r = 1.4$, $K = 216$, $C = 2$, $A = 12$, $g = 0.5$, and $D_o = 0.02$ (this parameter combination results in a single low-prey equilibrium).

D and F at their mean values. With this parameter set, the increase in the 1970s is an outbreak from the low equilibrium. The time series of herring biomass is too short to know the frequency of shifts between high and low abundances.

Discussion

The predator–prey model, coupled with highly autocorrelated environmental variability, is useful for describing the dynamics of pelagic fish stocks, such as the herring stock on the west coast of Vancouver Island. Classical biomass–dynamic models (Schaefer 1954), even when forced with autocorrelated random variability, would not be expected to exhibit the abrupt abundance changes characteristic of clupeoid populations. Thus, the predator–prey model we used includes nonlinear predation rates and the possibility of multiple population equilibria. While there may be other potential mechanisms for a nonlinear population response to environmental changes, there is evidence of Type III functional responses of vertebrate predators (Holling 1965).

Even though the model has two stable equilibrium configurations, the populations are by no means at equilibrium. Rather, environmental variability causes the populations to fluctuate within the domains of attraction, and prolonged environmental perturbations flip the populations from one domain of attraction to the other (Fig. 6b). A general feature of this predator–prey model is that relatively minor shifts in predator mortality translate into major shifts in prey abundance (Fig. 6). This model feature conforms with observations that populations of forage fishes are particularly prone to large-amplitude fluctuations (Lluch-Belda et al. 1989).

We extended the models of Steele and Henderson (1981, 1994) by explicitly including harvesting of the prey population. This formulation demonstrated the combined effects of environmental variability and fishing mortality on the prey population dynamics. Either increased predation or high fishing mortality can maintain the prey population at the low equilibrium level, and a relaxation of both sources of mortality may be necessary to boost the prey population to the upper equilibrium level. In summary, increased fishing mortality increased the proportion of time the prey population spent at the lower equilibrium level.

The main purpose of this paper was to describe a generic approach for incorporating environmental variability in population dynamics models. Therefore, we sought an example to illustrate the model, rather than selecting a model which best matched the dynamics of Pacific hake and Pacific herring. As a result, some assumptions of the predator–prey model are violated in the hake–herring example. In reality, the dynamics of hake and herring are loosely coupled. The hake distribution overlaps with that of the herring only seasonally, and even then, herring is not the only prey type in the hake diet. Thus, hake production is only partially dependent on herring abundance. The Type III predator functional response presumes the existence of an alternative food source even if the other prey species are not modeled explicitly. Mathematically, hake can be uncoupled from herring by replacing the first term in Equation 2 with gH. With production independent of prey, the pair of equations can be collapsed to a single prey equation without explicitly modeling the predator population (Collie and Spencer 1993). In the uncoupled model, the predator isocline in Fig. 3 would be horizontal. The triple-value region can still exist; the only difference is that the lower equilibrium point would be shifted. Whether or not predator production depends on prey has a minor effect on the prey dynamics.

In the model, environmental variability is introduced in the predator mortality rate (D). In the hake–herring example, SST variations are hypothesized to affect the degree of overlap between predator and prey. Thus, it may be more realistic to incorporate environmental variability in the consumption (C) term. Because of the form of the rescaled model

(Equations (3) and (4)), it is much easier to understand the effects of varying d or D than C. We suspect that adding environmental variability to the C parameter would also cause the populations to flip between domains of attraction, as it does in the single-species model (Collie and Spencer 1993). It is also possible that environmental variability is manifested through the pelagic food chain and directly affects the productivity (r and g) of herring and hake. The model dynamics are qualitatively similar if the autocorrelated variability is introduced in the r parameter instead of d (Steele and Henderson 1994).

Even though we included the dynamics of the predator (hake) in the model, in this application, we were primarily interested in the prey population. Because there is only a short time series for hake abundance in Canadian waters, we did not concentrate on fitting the model to these data. The hake population spends the greater part of the year outside Canadian waters and is no doubt influenced by factors outside our model. Year-to-year variability in Pacific hake recruitment has been related to upwelling and SST (Hollowed and Bailey 1989). We have shown that the variability in hake biomass has a red spectrum over a range of periods from 2 to approximately 60 yr. Thus, models of the entire hake population should incorporate long-term environmental forcing.

Even with a relatively simple predator–prey model, parameter estimation is difficult. Equations (1) and (2) contain six population parameters plus the fishing mortality rate, F. For stochastic simulations the two additional parameters in Equation 6 must be specified. In the direct fit of the model to the data there are the six population parameters to estimate, the initial values, P_0 and H_0, and a scaling factor between SST and D. It is infeasible to estimate all nine parameters with least-squares or maximum likelihood methods. Instead we matched the model output to the observed herring biomass by exploring the fit with many different parameter combinations.

Further refinements of the predator–prey model should make it more applicable to fish populations. A Type III functional response implies that the predator switches to an alternative prey at low densities of the primary prey species. An obvious extension is to include the alternative prey species (euphausids in the hake–herring example). Another high-priority development is to include fishing mortality on the predator population. The prey species equation can be modified to model competitive replacement, possibly mediated by the predator. Such models could address the apparent replacements observed in many species pairs (Daan 1980) and particularly between sardine (*Sardinops* spp.) and anchovy (*Engraulis* spp.) populations (Lluch-Belda et al. 1989; Sharp 1992). As any extensions to the basic model involve additional parameters to estimate, a careful balance must be maintained between realism and overparameterization.

Acknowledgments

We thank John Steele for encouraging this study and for reviewing the manuscript. Anne Hollowed kindly provided the SST data, Jake Schweigert the herring data, and Martin Dorn and Rick Methot the hake data. We thank the two anonymous reviewers for their reviews. This publication is the result of research sponsored by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration, Office of Sea Grant, Department of Commerce, under grant No. NA90AA-D-SG066 (project No. R/07-15).

References

AEBISCHER, N.J., J.C. COULSON, AND J.N. COLEBROOK. 1990. Parallel long-term trends across four marine trophic levels and weather. Nature (Lond.) 347: 753–755.

BAUMGARTNER, T.R., A. SOUTAR, AND V. FERREIRA-BARTRINA. 1992. Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments at the Santa Barbara basin, California. CalCOFI Rep., Vol. 33: 24–40.

COLLIE, J.S., AND P.D. SPENCER. 1993. Management strategies for fish populations subject to long-term environmental variability and depensatory predation, p. 629–650. *In* G.H. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn [ed.] Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations. Alaska Sea Grant College Program Rep. No. 93-02.

DAAN, N. 1980. A review of replacement of depleted stocks by other species and the mechanisms underlying such replacement. Rapp. P.-v. Réun. Cons. int. Explor. Mer 177: 405–421.

DORN, M.W., AND R.D. METHOT. 1993. Status of the coastal Pacific whiting resource in 1991. p. A1–A82. *In* Status of the Pacific coast groundfish fishery through 1991 and recommended acceptable biological catches in 1994. Pacific Fishery Management Council, Metro Center, Suite 420, 2000 SW First Ave., Portland, OR 97201.

HAIST, V., D.A. FOURNIER, AND J.F. SCHWEIGERT. 1993. Estimation of density-dependent natural mortality in British Columbia herring stocks through SSPA and its impact on sustainable harvesting strategies, p. 269–282. *In* S.J. Smith, J.J. Hunt, and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. int. Explor. Mer 20: 1–228.

HOLLING, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45: 1–59.

HOLLOWED, A.B. AND K.M. BAILEY. 1989. New perspectives on the relationship between recruitment of Pacific hake *Merluccius productus* and the ocean environment. p. 207–220. *In* R.J. Beamish and G.A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.

HOLLOWED, A.B. AND W.S. WOOSTER. 1992. Variability of winter ocean conditions and strong year classes of northeast Pacific groundfish. p. 433–444. *In* R.R. Dickson, P. Maelkki, G. Radach, R. Saetre, and M.P. Sissenwine [ed.] Hydrobiological variability in the ICES area, 1980–1989. ICES Mar. Sci. Symp. 195.

KAWASAKI, T., S. TANAKA, Y. TOBA, AND A. TANIGUCHI [ED.] 1991. Long-term variability of pelagic fish populations and their environment. Pergamon Press, Oxford.

LLUCH-BELDA, D., R.J.M. CRAWFORD, T. KAWASAKI, A.D. MACCALL, R.H. PARRISH, R.A. SCHWARTZLOSE, AND P.E. SMITH. 1989. Worldwide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci. 8: 195–205.

QUINN, T.J. II, AND J.S. COLLIE. 1990. Alternative population models for eastern Bering Sea pollock, p. 243–257. *In* L. Low [ed.] Proceedings of the Symposium on Application of Stock Assessment Techniques to Gadids. Int. North Pac. Fish. Comm. Bull. 50.

SCHAEFER, M.B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Bull. Inter-Am. Trop. Tuna Comm. 1: 27–56.

SCHWEIGERT, J.F., V. HAIST, AND C. FORT. 1993. Stock assessment for British Columbia herring in 1992 and forecasts of the potential catch in 1993. Can. Tech. Rep. Fish. Aquat. Sci. 1913: 111 p.

SHARP, G.D. 1992. Fishery catch records, El Niño/Southern Oscillation, and longer-term climate change as inferred from fish remains in marine sediments, p. 379–417. *In* H.F. Diaz and V. Markgraf [ed.] El Niño. Cambridge University Press, Cambridge, U.K.

SKUD, B.E. 1982. Dominance in fishes: the relation between environment and abundance. Science (Wash., DC) 216: 144–149.

SMITH, B.D., G.A. MCFARLANE, AND M.W. SAUNDERS. 1990. Variation in Pacific hake (*Merluccius productus*) summer length-at-age near southern Vancouver Island and its relationship to fishing and oceanography. Can. J. Fish. Aquat. Sci. 47: 2195–2211.

SMITH, P.E. 1978. Biological effects of ocean variability: time and space scales of biological response. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173: 117–127.

SOUTHWARD, A.J., G.T. BOALCH, AND G.T. MADDOX. 1988. Fluctuations

in the herring and pilchard fisheries off Devon and Cornwall linked to climate change since the 16th century. J. Mar. Biol. Assoc. U.K. 68: 423–446.

STATSCI. 1991. S-Plus users manual, Vol. 2. Statistical Sciences, Inc., Seattle, Wash.

STEELE, J.H. 1985. A comparison of terrestrial and marine ecological systems. Nature (Lond.) 313: 355–358.

STEELE, J.H., AND E.W. HENDERSON. 1981. A simple plankton model. Am. Nat. 117: 676–691.

STEELE, J.H., AND E.W. HENDERSON. 1994. Coupling between physical and biological scales. Philos. Trans. R. Soc. Lond. B 343: 5–9.

TANASICHUK, R.W., D.M. WARE, W. SHAW, AND G.A. MCFARLANE. 1991. Variations in diet, daily ration, and feeding periodicity of Pacific hake (*Merluccius productus*) and spiny dogfish (*Squalus acanthias*) off the lower west coast of Vancouver Island. Can. J. Fish. Aquat. Sci. 48: 2118–2128.

WALTERS, C.J., AND J.S. COLLIE. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45: 1848–1854.

WALTERS, C.J., M. STOCKER, A.V. TYLER, AND S.J. WESTRHEIM. 1986. Interaction between Pacific cod (*Gadus macrocephalus*) and herring (*Clupea hargengus pallasi*) in the Hecate Strait, British Columbia. Can. J. Fish. Aquat. Sci. 43: 830–837.

WARE, D.M., AND G.A. MCFARLANE. 1986. Relative impact of Pacific hake, sablefish and Pacific cod on west coast of Vancouver Island herring stocks. Int. North Pac. Fish. Comm. Bull. 47: 67–78.

WARE, D.M., AND R.E. THOMPSON. 1991. Link between long-term variability in upwelling and fish production in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 48: 2296–2306.

WOODRUFF, S.D., R.J. SLUTZ, R.L. JENNE, AND P.M. STEURER. 1987. A comprehensive ocean atmosphere data set. Bull. Am. Meteorol. Soc. 68: 1239–1250.

A Bayesian Approach to Stock Assessment and Harvest Decisions Using the Sampling/Importance Resampling Algorithm

Murdoch K. McAllister, Ellen K. Pikitch, Andre E. Punt, and Ray Hilborn

School of Fisheries WH-10, University of Washington, Seattle, WA 98195, USA

McAllister, M.K., E.K. Pikitch, A.E. Punt, and R. Hilborn. 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. Can. J. Fish. Aquat. Sci. 51: 2673–2687.

Scientific advice to fishery managers needs to be expressed in probabilistic terms to convey uncertainty about the consequences of alternative harvesting policies (policy performance indices). In most Bayesian approaches to such advice, relatively few of the model parameters used can be treated as uncertain, and deterministic assumptions about population dynamics are required; this can bias the degree of certainty and estimates of policy performance indices. We reformulate a Bayesian approach that uses the sampling/importance resampling algorithm to improve estimates of policy performance indices; it extends the number of parameters that can be treated as uncertain, does not require deterministic assumptions about population dynamics, and can use any of the types of fishery assessment models and data. Application of the approach to New Zealand's western stock of hoki (*Macruronus novaezelandiae*) shows that the use of Bayesian prior information for parameters such as the constant of proportionality for acoustic survey abundance indices can enhance management advice by reducing uncertainty in current stock size estimates; it also suggests that assuming historic recruitment is deterministic can create large negative biases (e.g., 26%) in estimates of biological and economic risks of alternative harvesting policies and that a stochastic recruitment assumption can be more appropriate.

L'avis scientifique destiné aux gestionnaires des pêches doit être exprimé en termes de probabilités afin de traduire l'incertitude au sujet des conséquences de divers régimes d'exploitation (indices de rendement). Dans la plupart des méthodes utilisant des estimateurs bayésiens pour formuler ces avis, relativement peu de paramètres du modèle peuvent être considérés comme incertains, et il faut des hypothèses déterministes concernant la dynamique des populations; ceci peut biaiser le degré de certitude et les estimations des indices de rendement. Nous avons reformulé une méthode bayésienne qui a recours à l'algorithme échantillonnage/importance rééchantillonnage pour obtenir de meilleures estimations des indices de rendement; elle augmente le nombre de paramètres qui peuvent être traités comme incertains, elle ne requiert pas d'hypothèses déterministes concernant la dynamique des populations, et peut utiliser n'importe quel type de modèles et de données d'évaluation de la pêche. L'application de la méthode au stock de hoki (*Macruronus novaezelandiae*) de l'ouest de la Nouvelle-Zélande montre que la méthode bayésienne utilisée avant l'obtention d'informations sur les paramètres comme la constante de proportionnalité des indices d'abondance obtenus par relevé acoustique peut donner un meilleur avis de gestion en réduisant l'incertitude des estimations actuelles de l'effectif du stock; elle semble indiquer également qu'en supposant déterministe le recrutement des années antérieures, elle peut créer d'importants biais négatifs (par exemple 26 %) dans les estimations des risques biologiques et économiques des autres régimes d'exploitation, et qu'une hypothèse de recrutement aléatoire convient peut-être mieux.

Received February 28, 1994
Accepted October 4, 1994
(J12293)

Reçu le 28 février 1994
Accepté le 4 octobre 1994

One of the key scientific inputs to fisheries management is the evaluation of the possible consequences (risks and rewards) of alternative harvest policies. It has become increasing recognized that such advice needs to be couched in probabilistic terms because of the unpredictable nature of fishery dynamics (Restrepo et al. 1992; Hilborn et al. 1993; Walters and Ludwig 1994; Walters and Punt 1994). A common and conceptually straightforward approach to providing such advice is Bayesian decision analysis (Raiffa 1968; DeGroot 1970; Berger 1985; Bergh and Butterworth 1987; Sainsbury 1988; Collie and Walters 1991; Thompson 1992; Hilborn et al. 1994; Walters and Punt 1994). For each possible state of nature, for example, current stock size, the consequences of each alternative management action are evaluated, and summarized by means of performance indices such as total catch. The probabilities of each state of nature are obtained from a stock assessment. The performance indices are then weighted by the probability of each alternative state of nature to provide the expected values of each performance index for each candidate management action. Once applied, the Bayesian approach can enable analysts to provide graphical and easy-to-interpret displays of (1) uncertainty, in the form of probability distributions for key quantities of interest (current stock size), and (2) accompanying estimates of risks and benefits of the alternative actions that can be taken.

Non-Bayesian approaches that apply Monte Carlo or bootstrap methods can also be used to evaluate harvesting policies (Francis 1992; Francis et al. 1992; Restrepo et al. 1992, 1993). The main assumptions invoked for estimating probability

distributions for quantities of interest vary considerably among the Bayesian and non-Bayesian procedures and can potentially cause differences in estimation performance and versatility in providing management advice (i.e., quality of management advice). However, there exists no consensus about which approach is better (Cordue and Francis 1994; Walters and Ludwig 1994).

Among the Bayesian procedures for fisheries decision analysis, differences in implementation can potentially result in large differences in estimation performance. We first provide a brief overview of some of the chief differences in implementation and assumptions among the various Bayesian procedures. We then suggest a reformulation of a highly versatile Bayesian procedure that can enhance the quality of fishery management advice that is provided.

Most Bayesian procedures for fisheries decision analysis admit uncertainty in only a fraction of the model parameters used and assume that all of the others such as natural mortality rate, historic recruitment anomalies, and/or stock–recruit parameters are known without error (Sainsbury 1988; Collie and Walters 1991; Thompson 1992; Hilborn et al. 1994; Walters and Ludwig 1994). Deterministic assumptions about population dynamics are typically required by such procedures. While useful for illustrative purposes and when data are relatively sparse, admitting uncertainty in only a few of the model parameters and ignoring uncertainty in others is usually not desirable because it underrepresents uncertainty and can introduce bias in risk assessments. It is desirable then to develop a Bayesian procedure for fisheries decision analysis that can incorporate uncertainty in all model parameters.

A key output of Bayesian assessment is the posterior probability density function (pdf) of the parameters of interest. This summarizes the uncertainty in all uncertain model parameters after analyzing the data (see below for more details). Bayesian approaches that admit uncertainty in relatively few parameters construct posterior pdfs in one of three different ways. The first is analytically (e.g., Thompson 1992). The second is by calculating the posterior probability at each point in a grid of parameter combinations (Hilborn et al. 1994). The third is by integrating over nuisance parameters before using this grid approach (Walters and Ludwig 1994; Walters and Punt 1994). However, as the number of parameters to be treated as uncertain increases, calculating posteriors with such procedures becomes intractable. Monte Carlo approaches for estimating posterior pdfs are then required. These include Markov Chain methods (e.g. the Gibbs sampler) and importance sampling (e.g. the sampling/importance resampling (SIR) algorithm) (Berger 1985; Rubin 1987, 1988; Smith 1991; West 1993). Monte Carlo Bayesian methods have been applied in relatively few instances (Bergh and Butterworth 1987; Francis et al. 1992; Givens et al. 1993; Kinas 1993; Punt et al. 1994).

Bergh and Butterworth (1987) presented a Monte Carlo Bayesian method for fisheries decision analysis that generates multiple future projections of age structure using vectors of parameters that are randomly drawn from a joint prior pdf (the prior pdf represents uncertainties in parameter values prior to evaluating the data — see below). The method can consider both short- and long-term horizons and a wide variety of harvesting policies and performance indicators. However, the procedure for computing the joint posterior pdf is described in the context of a population dynamics model that assumes constant mean recruitment and a pulse fishery on recruits and, as described, is not easily generalized to situations with multiple age-classes and more typical stock–recruit functions (e.g., Ricker and Beverton–Holt).

We reformulate the highly versatile SIR algorithm to estimate Bayesian probability distributions for quantities of interest in stock assessment and harvest decisions. The algorithm can include (a) either a non-age-structured population dynamics model or an age-structured one with a stock–recruit function, (b) process error (e.g., stochasticity in recruitment), and (c) uncertainty in as many model parameters as desired. We illustrate the algorithm using New Zealand's western stock of hoki (*Macruronus novaezelandiae*) for which data on relative abundance and year-class strengths of individual cohorts are available. Using the example, we develop some new empirical approaches to constructing informative prior pdfs that use expert judgment and large data sets on related species. The example also demonstrates the importance of incorporating process error and informative versus noninformative priors for model inputs in Bayesian stock assessment and decision analysis of alternative harvesting policies.

Defining the Conceptual Framework for a Bayesian Stock Assessment

In a Bayesian stock assessment, a population dynamics model is fit to data (e.g., relative indices of abundance) in order to construct a posterior pdf of model parameters. For example, if an age-structured model is used, model parameters could include stock–recruit model parameters (e.g., the average unexploited biomass, B_o), natural mortality rate (M), the extent of recruitment variability (σ_r), and the historic recruitment anomalies (ϵ_y) that together determine the age structure at the start of the current year (i.e., year in which the harvest decision is to be made). A vector or set of model parameters that are considered jointly will be referred to as θ. A state of nature is one potential realization of the set of all possible values for θ, say θ_i. The posterior pdf of θ is used to construct additional probability distributions, and to make inferences about quantities that are of use in making harvest decisions (e.g., biological and economic risks).

Using Prior Probabilities in Bayesian Assessments

One of the key features of Bayesian analysis is the use of prior probabilities (Box and Tiao 1973; Berger 1985). A prior $p(\theta_i)$ conveys the probability that a given state of nature (θ_i) is true prior to obtaining a set of data that can further our ability to discriminate among alternative θ's. Once the data have been obtained, they are used together with the priors in Bayes theorem to compute the posterior probability, the probability that a given state of nature i is true conditioned on the data, $P(\theta_i|\text{data})$:

$$(1) \quad P(\theta_i \mid \text{data}) = \frac{L(\text{data} \mid \theta_i)p(\theta_i)}{\int L(\text{data} \mid \theta)p(\theta)d\theta}$$

where $L(\text{data}|\theta_i)$ is the likelihood function for the data evaluated at θ_i. When data contain little information, the posterior pdf tends to reflect the prior pdf. However, as data become more informative, $L(\text{data}|\theta_i)$ predominates and priors lose their influence over the posterior.

The procedure that is presented in this paper uses a joint prior pdf of multiple model input parameters (see below). For simplicity, the prior in the example application assumes that the parameters are all independent of each other. For example, prior to evaluating the data, no combinations of values for B_o and M are assumed to be more credible than others when these two parameters are considered jointly (see Discussion). Therefore, the joint prior is simply the product of the priors for each of the individual parameters and these priors are constructed separately for each parameter.

Two types of priors that can be used are "noninformative" and "informative" priors. Informative priors typically convey some prior knowledge about a parameter. In contrast, noninformative priors have been used to alleviate concerns over the role of subjectivity in the choice of priors and their influence over the posterior (see DeGroot 1970; Box and Tiao 1973; Berger 1985). Noninformative priors convey ignorance (or objectivity) with respect to parameters of interest and "let the data speak for themselves". Noninformative priors are also sometimes constructed for "nuisance" parameters (parameters that must be included but are not of interest) and are used in combination with informative priors (Box and Tiao 1973). Here, noninformative priors are chosen for nuisance parameters so that when the data contain little information, the marginal posteriors for key parameters reflect their priors (see Box and Tiao 1973; Berger 1985). For example, suppose the average unexploited biomass, "B_o", is a key parameter and has an informative prior, and the scale parameter between relative abundance indices and predicted biomass "q", is a nuisance parameter. A noninformative prior for q is chosen (which may not be uniform over q) so that the marginal posterior for B_o (the joint posterior integrated with respect to q) is the same as its prior when the data are uninformative (see below).

If there is very little information about a parameter, it is appropriate to use a noninformative prior. However, the construction of informative priors is desirable wherever possible because it can help to improve estimation performance. Even then, noninformative priors can be used to evaluate the impacts on posteriors of informative priors versus the data alone, absent of prior knowledge or bias (Box and Tiao 1973).

Using Sampling/Importance Resampling to Construct Probability Distributions for Quantities of Interest

When there are several uncertain parameters in a Bayesian assessment, a Monte Carlo procedure is usually required to estimate the posterior pdf of them. A sample from this distribution can be used to estimate probability distributions for quantities of interest that are known functions of the parameters in the posterior. The SIR algorithm has been proposed as one of the simplest, most versatile Bayesian Monte Carlo methods for drawing a sample from the posterior (Rubin 1987, 1988; Smith 1991).

The SIR algorithm can be used where it is possible to generate a sequence of i.i.d. random variables (θ_1, θ_2, θ_3,...) that have a common probability density, $h(\theta)$, called an "importance function" (Berger 1985). The reason for using $h(\theta)$ in the algorithm can be understood by starting with the posterior expectation, $E^{P(\theta|\text{data})}[g(\theta)]$, of some function of the random variables, $g(\theta)$ (for example, $g(\theta)$ could be fish stock size in the current year as a function of B_o and other parameters). Using equation 1:

$$(2)\quad E^{P(\theta|\text{data})}[g(\theta)] = \frac{\int g(\theta)L(\text{data}\mid\theta)p(\theta)d\theta}{\int L(\text{data}\mid\theta)p(\theta)d\theta}.$$

The SIR algorithm uses the following identity in order to estimate a posterior pdf of θ:

$$(3)\quad \int g(\theta)L(\text{data}\mid\theta)p(\theta)d\theta = \int \frac{g(\theta)L(\text{data}\mid\theta)p(\theta)h\theta}{h(\theta)}\,d\theta$$

$$= E^{h(\theta)}\left[\frac{g(\theta)L(\text{data}\mid\theta)p(\theta)}{h(\theta)}\right].$$

Using some i.i.d. sequence of m random variables (θ_1, θ_2,..., θ_m) with common density $h(\theta)$, and the strong law of large numbers it follows that, under mild conditions (Berger 1985, p. 263):

$$(4)\quad \lim_{m\to\infty}\frac{1}{m}\sum_{k=1}^{m}\left[\frac{g(\theta_k)L(\text{data}\mid\theta_k)p(\theta_k)}{h(\theta_k)}\right]$$

$$= \int g(\theta)L(data\mid\theta)p(\theta)d(\theta).$$

This identity can be used to approximate the numerator and denominator in equation 2:

$$(5)\quad E^{P(\theta|\text{data})}[g(\theta)] \cong \frac{\sum_{k=1}^{m} g(\theta_k)w(\theta_k)}{\sum_{k=1}^{m} w(\theta_k)}$$

where the "importance ratios", $w(\theta_k) = \dfrac{L(\text{data}\mid\theta_k)p(\theta_k)}{h(\theta_k)}$.

This approximation improves as m increases. Thus, importance sampling, the process of generating θ_k according to $h(\theta)$, forms a discrete distribution over (θ_1, θ_2,..., θ_m) placing mass

$$P(\theta_k\mid\text{data}) \cong \frac{w(\theta_k)}{\sum_{k=1}^{m} w(\theta_k)}$$

on each θ_k. This distribution is taken as an estimate of the actual posterior distribution. A key task of importance sampling is that of finding a suitable $h(\theta)$ (see Berger 1985).

In order to estimate distributions for quantities of interest that are known functions of θ, a random sample of size n with $n < m$ is taken from the estimated posterior distribution over (θ_1, θ_2,..., θ_m). This step is the resampling part of the SIR algorithm.

The SIR algorithm has been applied in few fisheries assessments (e.g., Francis et al. 1992; Givens et al. 1993). In a study that was not explicitly Bayesian, Francis et al. (1992) used a simple version of the SIR algorithm in order to calculate the biological risks of alternative harvesting policies for orange roughy (*Hoplostethus atlanticus*). Prior-like distributions were used for only two of several types of the population model parameters used (i.e., B_o and recruitment anomalies); the rest were assumed known without error. Givens et al. (1993) used the SIR algorithm (Rubin 1987, 1988) in order to estimate probability distributions for bowhead whale population parameters. The procedure used a

deterministic population dynamics model and estimated quantities relating to the current status of the population such as the replacement yield in the current year. Below, we reformulate the SIR algorithm in order to provide the flexibility to incorporate process error (e.g., random variability in recruitment) and to enable a full decision analysis of alternative harvesting policies.

(1) Start by choosing an importance function $h(\theta)$, i.e., a joint probability density function of the model input parameters, θ. Berger (1985) recommended that for computational efficiency, it is best to choose $h(\theta)$ such that it is as close to the posterior pdf as possible. For example, if the likelihood function is itself a density in θ, the likelihood function (after normalization) can sometimes be a good choice for $h(\theta)$. However, for simplicity, the prior distribution $p(\theta)$ is sometimes used as the importance function (e.g., Givens et al. 1993; Kinas 1993; Punt et al. 1994).

(2) Draw one set of values θ_k for the model inputs from $h(\theta)$ (k refers to draw number k, since this step is repeated many times). For example, if an age-structured procedure is to be used and if the prior is to be used as the importance function, draw one set of values for B_0, M, and σ_r from their joint prior. If process error is to be included and input parameters are considered to be independent, then for each of the cohorts which have been, or will be, subject to fishing, draw a value for a recruitment residual, ϵ_y, from, e.g., a normal pdf with mean r_y and standard deviation (SD) σ_r (see equation I.3).

(3) Project the population dynamics model once from virgin, unfished conditions forward to the current year (e.g., see Appendix I), using the values of model inputs, θ_k, drawn in step 2 and the known catches to predict stock biomass and any other model quantities that can be fitted to available data. (For the kth draw from $h(\theta)$, the projection of the model from unfished conditions up to the current year will be referred to as historic trajectory k.)

(4) Evaluate the likelihood function, $L(\theta_k|\text{data})$, mass of the prior, $p(\theta_k)$, and mass of the importance function, $h(\theta_k)$, for the kth draw from $h(\theta)$, i.e., historic trajectory k (e.g., see Appendix II).

(5) If any of the exploitation rates rise above the maximum possible (e.g., see equation I.12), $p(\theta_k)$ is set to zero.

(6) Calculate the importance ratio, $w(\theta_k)$, for historic trajectory k:

$$w(\theta_k) = \frac{L(\theta_k|\text{data})p(\theta_k)}{h(\theta_k)}.$$

Note that if the importance function is set equal to the prior pdf, $h(\theta) = p(\theta)$, then

$$w(\theta_k) = \frac{L(\theta_k|\text{data})p(\theta_k)}{p(\theta_k)} = L(\theta_k|\text{data}).$$

(7) Repeat steps 2 to 6 a very large number of times (e.g., m = 20 000). The posterior pdf of θ is estimated by normalizing the importance ratios:

$$(6)\quad \hat{P}(\theta_k|\text{data}) = \frac{w(\theta_k)}{\sum_{j=1}^{m} w(\theta_j)}$$

where $\hat{P}(\theta_k|\text{data})$ is the estimated posterior for trajectory k. The set of nonzero values for $\hat{P}(\theta_k|\text{data})$ represents the estimated joint posterior pdf of θ.

(8) Draw a large number (e.g., n = 5000) of θ_k randomly with replacement from $(\theta_1, \theta_2, \ldots, \theta_m)$ with probabilities proportional to $w(\theta_1), w(\theta_2), \ldots, w(\theta_m)$. The resulting sample $(\theta_1, \theta_2, \ldots, \theta_n)$ approximates an i.i.d. sample from the joint posterior pdf of θ. This sample is used when performing the decision analysis (see below).

Marginal posterior pdfs of parameters of interest, such as B_0, or current stock size, B_{cur}, are obtained by integrating the joint posterior pdf with respect to all other parameters. A simple histogram-type density estimator can be used to estimate marginal distributions. Technically, the marginal pdf of current stock size, for example, is computed by first choosing an appropriate step size, 100 kt, for example, and upper and lower bounds for the pdf, and then computing the total probability in each step or "bin":

$$(7)\quad \hat{P}(B_{cur,i_L} < B_{cur} \le B_{cur,i_U}) = \sum_{k=1}^{m} \hat{P}(\theta_k|\text{data})I_i$$

where $\hat{P}(B_{cur,i_L} < B_{cur} \le B_{cur,i_U})$ is the estimated marginal probability that B_{cur} lies within bin i, $\hat{P}(\theta_k|\text{data})$ is the joint posterior probability for the vector of parameter values in historic trajectory k, $I_i = 1$ if $B_{cur,i_L} < B_{cur,k} \le B_{cur,i_U}$ and 0 otherwise, and $B_{cur,k}$ is the value for Bcur in trajectory k. Another approach would be to use a nonparametric kernal density estimator or some other smoothing estimator (Silverman 1986). This could provide more precise, accurate estimates of marginal distributions.

Calculating the Consequences of Harvesting Options

For each of the historic trajectories (or θ_k) that are drawn in step 8 above, a future projection is carried out in order to evaluate harvesting options. Note that, because a historic trajectory may be selected more than once, it is possible for multiple future projections to be performed for a single set of model inputs. Each of these projections considers a different set of process errors (e.g., future recruitment residuals (ϵ_y: $y > 1993$)) even though the values of the model parameters and historic process errors (historic recruitment residuals) remain the same. Each future projection involves applying the management policy under consideration to set the total allowable catch (TAC) for a specific time frame, e.g., 5 yr.

Performance statistics for each policy are calculated during each future projection. These statistics may be particular to each year in the sequence if, for example, the immediate consequences of this year's and next year's quotas are of interest. The statistics can also be averaged across all years if the overall attributes of the harvesting options are of interest. The expected value $x(V_{p,x})$ for each statistic and policy p is computed from

$$(8)\quad \hat{E}(V_{p,x}) = \frac{1}{n}\sum_{i=1}^{n} V_{p,x,i}$$

where n is the total number of future projections (5000) and $V_{p,x,i}$ is the value of statistic x for policy p in future projection i.

In order to convey the uncertainty in model results to decision makers, the performance statistics can be reported for discrete ranges or "bins" for a given parameter, Q, of interest. The expected value of performance statistic x for policy p in bin j ($\hat{E}(V_{p,x,j})$) is computed from

$$(9)\quad \hat{E}(V_{p,x,j}) = \frac{1}{\sum_{i=1}^{n} I_j} \sum_{i=1}^{n} I_j V_{p,x,i}$$

where $I_j = 1$ if $Q_{j,L} < Q_i \leq Q_{j,U}$ and 0 otherwise, Q_i is the value for the parameter in future projection i, and $Q_{j,L}$ and $Q_{j,U}$ are the lower and upper bounds to bin j.

Uncertainty, Risks, and Rewards: Application to New Zealand Hoki

The procedure described above has been applied to data for New Zealand's western stock of hoki. The exploitation history and data series on relative abundance are relatively short and there is large uncertainty over current stock size and the amount of depletion from unexploited conditions that has occurred (Sullivan 1994). The fishery is managed by individual transferable quota and there is currently interest in evaluating both short- and long-term consequences of alternative harvest policies.

Assessment Procedure

Only the key features of the assessment procedure are described here, since the details are not important for understanding the use of the numerical procedure (see Punt et al. 1993b, 1994 for the details).

Population dynamics model

The population dynamics model used for assessing risks and benefits of alternative harvesting policies was originally developed for application to fisheries in New Zealand where detailed age-structured population dynamics models have been preferred (Francis 1992; Cordue 1993). Such models have been applied in other cases where available information included (a) estimates of natural mortality rates and mass-, vulnerability-, and fecundity-at-age, (b) catch history, and (c) occasional indices of abundance (Francis 1992; Francis et al. 1992; Punt et al. 1993a; Hilborn et al. 1994). Unlike biomass dynamic models, these models can be fit to data that reflect recruitment fluctuations (e.g., Francis et al. 1992). These models are also easily modified to incorporate peculiarities of the biology or seasonal harvest operations (Hilborn and Walters 1992). In addition, models of this type may be more credible to parties involved in decision making, particularly those who are not mathematically inclined, than simpler less versatile models. Finally, such models are capable of producing almost any policy performance index that is of interest. For example, bioeconomic attributes such as the fraction of marketable-sized individuals in future catches can be readily estimated. The parties to decision making can thus use the indices of greatest interest to them, and will not be confined to ones that may be difficult to interpret or bear little relationship to perceived future needs or goals as might happen when more restrictive models are used (e.g., biomass dynamics (Sainsbury 1988) or delay-difference models (Collie and Walters 1991)). An approach that incorporates model flexibility can thereby facilitate increased participation, e.g., of industry members, in harvest decisions and help to make the decisions more accountable to them.

We selected a fully age-structured model because we believed it to be the most appropriate choice in this case, given the factors described above. We considered a biomass dynamic model inappropriate for the present analysis because it cannot account for recruitment fluctuations that are reflected in the available age-structured data (see below). These data could have been incorporated in a delay-difference type model. However, this alternative is just an algebraic reduction of a full age-structured model. It has the same types of costs and benefits as a fully age-structured model but is not as flexible or intuitively appealing to decision makers.

The population dynamics model that is used is detailed in Appendix I. The model is age and sex structured and assumes that annual recruitment is log-normally distributed about the Beverton–Holt function. Any other stock–recruit function can be easily substituted. The model also specifies for each age-class a fixed fraction of individuals that will recruit annually to the fishery from the unrecruited population.

TABLE 1. Indices of relative abundance and their associated (assumed) CVs used in the assessments of the western stock of hoki. The CVs include contributions from sampling error and other sources.

	Acoustic		CPUE		Trawl survey	
Year	Index	CV	Index	CV	Index	CV
1983	—	—	—	—	1.00	0.45
1984	—	—	—	—	—	—
1985	—	—	—	—	—	—
1986	—	—	—	—	—	—
1987	—	—	1.335	0.35	—	—
1988	274	0.28	1.000	0.35	—	—
1989	171	0.22	0.604	0.35	0.72	0.45
1990	160	0.21	0.493	0.35	0.94	0.45
1991	259	0.25	0.484	0.35	1.18	0.25
1992	218	0.28	0.636	0.35	1.96	0.25

Types of data used

The population dynamics model (Appendix I) was fitted to three types of relative abundance data that represent different age-class groupings: one from acoustic surveys, a second from catch per unit effort (CPUE) of the commercial fleet, and a third from trawl surveys (see Table 1 for the values and their coefficients of variation (CVs) and Appendix I (E) for details). The first two represent only mature recruited fish that have gone to spawn; the latter represents all fish age 4+ after the spawning season. While they are not fully age structured, taken together, these indices can to some extent reflect the year-class strengths of individual cohorts, particularly if there are some very large or small year-classes. The biomass data of commercial catches include two series, one for catches taken year-round south of the South Island, and a second for catches taken from winter spawning aggregations on the west coast of the South Island (Appendix I (A and D); Fig. 1). In order to fit an age-structured model to such data, it is necessary to assume that the fraction of fish harvested in each recruited age-class is equal to the ratio of the observed catch biomass to the predicted exploitable biomass and that the catch biomass series is known without error (see equation I.11) (Francis 1992; Francis et al. 1992; Punt et al. 1993a; Hilborn et al. 1994).

Priors used

The method incorporated informative prior pdfs of virgin biomass (B_o), steepness (h, reflecting the expected fraction of virgin recruitment at $0.2B_o$ (equation I.8)), recruitment

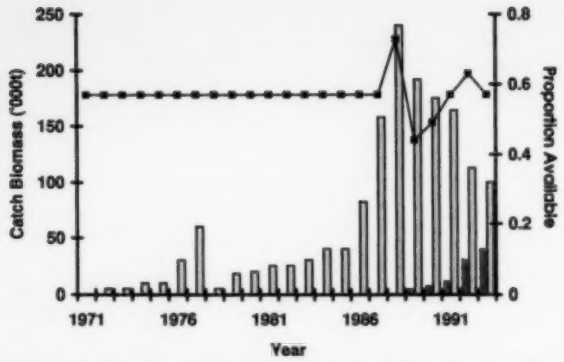


FIG. 1. Catch biomass series for New Zealand's western stock of hoki. One is for a winter fishery on spawning aggregations on the West Coast South Island (lightly stippled bars). The other is for a year-round fishery on the Southern Plateau (heavily stippled bars). The proportion of spawner biomass in the open area is also shown (see equation I.12).

variability (σ_r), year-class strengths for the 1987 and 1988 cohorts (ϵ_y in equation I.3), natural mortality rate (M), and the constant of proportionality which relates the acoustic estimates of the spawner biomass to actual spawner biomass (q_1) (see Table 2). It is assumed that B_0 is uniformly distributed over the interval 0–3000 kt. The prior pdfs of M (Table 2) are based on the range used in the tests of the sensitivity of the results to the value of this parameter in Cordue (1993). The prior pdf of σ_r is log-normal with a median of 0.65 and a CV of 0.3 (Table 2). This prior is based on maximum likelihood estimates of this parameter for haddock, hake, pollock, whiting, and cod in the North Atlantic obtained from the synthesis study of Myers et al. (1990), and an analysis of hoki length–frequency data (Sullivan 1994). The priors for year-class strengths (ϵ_y) are also based on analysis of hoki length–frequency data (Sullivan 1994).

The prior pdf of q_1, is log-normal with a median of 0.503 and a CV of 0.715 (Table 2). This prior pdf was constructed by Monte Carlo simulation of the uncertainties in mean target strength per fish, and nine other variables, associated with the acoustic estimates of abundance (details in Punt et al. 1994).

It is currently not possible to construct informative prior pdfs of the constants of proportionality (q) for the CPUE and trawl survey indices. Instead, the priors for these parameters have been taken to be noninformative with respect to B_0. For scale parameters (e.g., σ) in density functions such as the normal or log-normal, the appropriate noninformative prior is one which is uniform on a log scale (see Jeffreys 1961; Box and Tiao 1973; Bernardo 1979; Berger 1985). Because a constant of proportionality that relates a biomass index to a model quantity takes the form of a scale parameter in the likelihood function assumed (Appendix II), this same noninformative prior applies and was used (Table 2).

In the 1993 assessment, a point prior for steepness (h) (equation I.8) was assumed, i.e., $h = 0.75$. Following the assessment, an empirical prior was constructed based on the following assumptions: (a) the steepness of the hoki stock–recruitment relationship (h_{hoki}) is equal to the steepness of the stock–recruitment relationship for some gadoid, (b) the

TABLE 2. "Base case" priors of some population dynamics model parameters (see Appendix I) used in the 1993 assessment of the western stock of hoki (source; Punt et al. 1993b).

Parameter	Prior
B_0 ('000 t)	$U[0, 3000]$
Steepness, h	$h = 0.75$
σ_r	Log-normal: median = 0.65, SD = 0.3
ϵ_{1987}, ϵ_{1988}	0.45, 3.55 (equation I.3)
M (yr^{-1})	$M^m \sim U[0.25, 0.35]$, $M^f \sim U[0.2, 0.3]$
q(acoustic)	Log-normal: median = 0.503, SD = 0.715
q(trawl)	$\log(q) \sim U[-\infty,\infty]$
q(CPUE)	$\log(q) \sim U[-\infty,\infty]$

particular gadoid is unknown, but the probability of it being any one of those for which stock–recruit data are available (say gadoid j) is the same ($P(h_{\text{hoki}} = h_{\text{gadoid}_j})$ = constant = $1/N$ where N is the total number of gadoids for which stock–recruit data are available), and (c) a prior for steepness (before looking at the data) would be $U(0.2, 1)$. Now, the probability that h_{hoki} is equal to that for gadoid j and that h_{hoki} equals one of a discrete number of alternatives values for steepness (h_i) is equal to the probability that $h_{\text{hoki}} = h_{\text{gadoid}_j}$ times the conditional probability that $h_{\text{hoki}} = h_i$ given that $h_{\text{hoki}} = h_{\text{gadoid}_j}$:

$$P[h_{\text{hoki}} = h_{\text{gadoid}_j} \text{ and } h_{\text{hoki}} = h_i] = P[h_{\text{hoki}} = h_{\text{gadoid}_j}]P[h_{\text{hoki}} = h_i \mid h_{\text{hoki}} = h_{\text{gadoid}_j}].$$

Therefore, the probability that $h_{\text{hoki}} = h_i$ is given by

$$P[h_{\text{hoki}} = h_i] = \sum_{j=1}^{N} P[h_{\text{hoki}} = h_{\text{gadoid}_j}]P[h_{\text{hoki}} = h_i \mid h_{\text{hoki}} = h_{\text{gadoid}_j}].$$

From assumptions (a) and (b) above, this means that

$$P[h_{\text{hoki}} = h_j] = \frac{1}{N}\sum_{j=1}^{N} P[h_{\text{hoki}} = h_i \mid h_{\text{hoki}} = h_{\text{gadoid}_j}].$$

The conditional probability for gadoid stock j is calculated by normalizing the likelihood profile for h for that stock (i.e., making use of assumption (c)). Likelihood profiles were computed using stock–recruit data provided by N. Barrowman and R. Myers (Science Branch, Department of Fisheries and Oceans, St. John's, Nfld.) (data summarized in Myers et al. 1993). When constructing this prior for steepness, only those gadoid stocks for which at least 10 stock and recruitment data points are available were used. Further details are provided in Punt et al. (1994). The resulting prior is shown in Fig. 2.

The simulation procedure selected 5000 of the 20 000 historic trajectories to calculate future projections. The base case application of the stock assessment technique used the relative abundance indices in Table 1, the catch biomass series shown in Fig. 1, the priors in Table 2, and the biological and technological parameters in Table 3.

Bayesian estimates of stock status: evaluating the effects of priors

Bayesian estimates of uncertainty in the status of hoki are conveyed by using marginal posterior pdfs of current-year

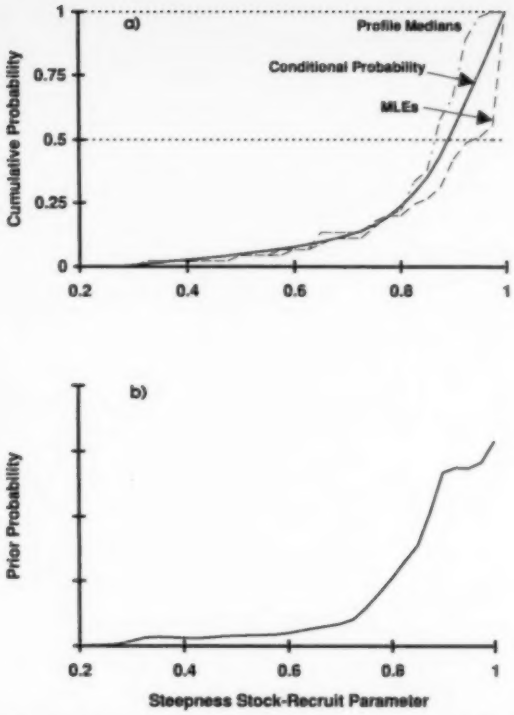


FIG. 2. (a) Cumulative distribution (cd) for an informative prior for the steepness parameter (h) in the Beverton–Holt stock–recruit function based on the theorem of conditional probability and stock–recruit data for 43 gadoid stocks in Myers et al. (1993) (see text). Also shown are cumulative frequency distributions for the medians of the likelihood profiles used and the MLEs of h for these data. (b) Prior pdf of h.

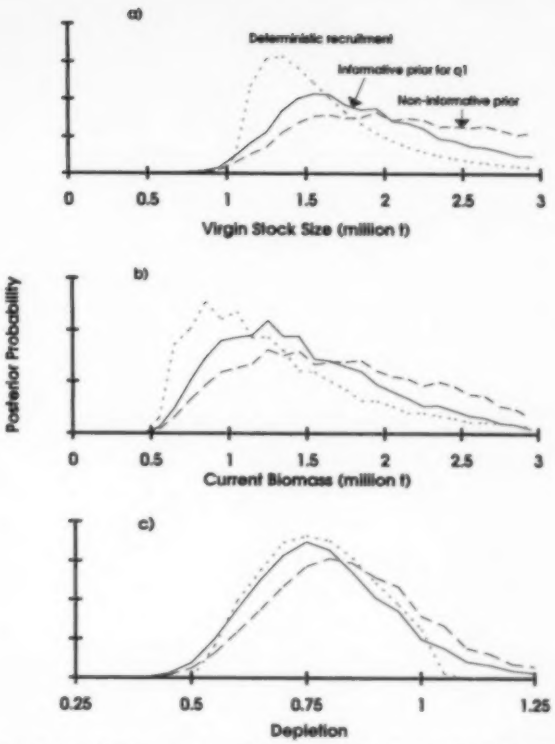


FIG. 3. Marginal posterior pdfs of (a) B_0, (b) B_{cur}, and (c) B_{cur}/B_0 using noninformative and informative (base case) priors for the constant of proportionality (q_1) for acoustic survey indices. Posteriors for the case with deterministic recruitment, known values for M, and an informative prior for q_1 are also shown.

(1993) midseason stock size (B_{cur}), virgin stock size (B_0), and the amount of depletion (B_{cur}/B_0) (Punt et al. 1993b). Nine tests were conducted to assess the sensitivity of the posteriors to assuming either stochastic or deterministic recruitment and assuming either point priors (i.e., assuming that parameters are known without error, as is commonly done), noninformative priors, or informative priors. These tests are as follows: (1) replacing the informative prior for the constant of proportionality for the acoustic indices by a noninformative prior; (2) assuming that recruitment is deterministic (i.e., $\sigma_r = 0$) and replacing the priors for M by fixed values ($M^m = 0.3 \cdot yr^{-1}$, $M^f = 0.25 \cdot yr^{-1}$); (3) replacing the priors for M with a $U(0.01,3)$ prior; (4) replacing the prior for σ_r with a $U(0,3)$ prior; (5) replacing the priors for M and σ_r by fixed values ($M^m = 0.3 \cdot yr^{-1}$, $M^f = 0.25 \cdot yr^{-1}$, and $\sigma_r = 0.65$); (6) assuming that steepness = 0.95; (7) assuming that steepness = 0.5; (8) assuming a prior for steepness that is $U(0.2, 1.0)$; (9) assuming an informative prior for steepness (Fig. 2).

Estimating the consequences of alternative harvesting options

For each of those historic trajectories which were selected, a further 5-yr horizon was carried out to evaluate various harvesting options. Each future projection involves applying the management policy under consideration to set the TAC for the next 5 yr (i.e., 1994–98; the TAC for 1993 is always taken to be 140 kt).

Six tests were conducted to assess the sensitivity of decision analysis results to assuming either deterministic or stochastic

TABLE 3. Values of the model parameters used in the assessments of the western stock of hoki (source: Sullivan 1994).

Parameter	Male	Female
Fraction spawning,		
μ (%)	N/A	70
L_∞ (cm)	102.8	112
κ (yr^{-1})	0.199	0.172
t_0 (yr)	−1.01	−1.13
δ_1 ($gm \cdot cm^{-3}$)	0.006	0.006
δ_2	2.85	2.85
Plus-group, m (yr)	20	20
F_{crit}	See equation I.12	See equation I.12
Max. catch/biomass, ϕ	0.8	0.8
ϕ_1^s	0	0
ϕ_2^s	0	0
ϕ_3^s	0	0.0714
ϕ_4^s	0.0714	0.4290
ϕ_5^s	0.4290	1
ϕ_{6+}^s	1	1

TABLE 4. Estimates of means and standard deviations (in parenthesis) using marginal posterior pdfs of B_0, B_{1993}, $\%B_{1993}/B_0$ for the base case stock assessment and the sensitivity tests. Biomass units are '000 t.

Application	B_0	B_{1993}	$\%B_{1993}/B_0$
Base case	1863 (480)	1502 (559)	79.6 (16.1)
Noninformative acoustic prior	2050 (517)	1752 (679)	85.3 (18.1)
Deterministic recruitment, M known	1625 (419)	1310 (546)	77.6 (11.9)
Prior for $M \sim U(0.01,3)$	1778 (541)	1739 (748)	98.5 (29.6)
Prior for $\sigma_r \sim U(0,3)$	1967 (514)	1517 (573)	77.2 (19.3)
M, σ_r known	1855 (470)	1505 (555)	79.7 (15.0)
Steepness (h) = 0.95	1839 (480)	1514 (563)	81.1 (15.6)
h = 0.5	1920 (482)	1475 (553)	76.1 (17.6)
Prior for $h \sim U(0.2,1)$	1900 (487)	1489 (560)	77.8 (18.4)
Informative prior for h (Fig. 2)	1853 (481)	1507 (562)	80.2 (16.1)

TABLE 5. Policy performance indices for the base case scenario. The acronyms for the performance indices are defined in Appendix III. Biomass units are '000 t.

Statistic/policy	Risk (stock)	Risk (fishery)	Catch	$E(B_{fin}/B_{MSY})$	$P(B_{fin} > B_{MSY})$	Catch loss
150-kt constant quota	0.012	0.003	148	2.455	0.974	0
200-kt constant quota	0.052	0.038	189	2.087	0.899	−5
250-kt constant quota	0.112	0.148	227	1.779	0.786	−13
300-kt constant quota	0.119	0.318	258	1.524	0.671	−23
350-kt constant quota	0.235	0.494	283	1.336	0.585	−39
400-kt constant quota	0.279	0.646	302	1.203	0.517	−48

recruitment and to assuming either point priors, noninformative priors, or informative priors. These tests are as follows: (1) replacing the informative prior for the constant of proportionality for the acoustic indices by a noninformative prior; (2) assuming that historic and future recruitment is deterministic (i.e., $\sigma_r = 0$) and replacing the priors for M by fixed values ($M^m = 0.3 \cdot yr^{-1}$, $M^f = 0.25 \cdot yr^{-1}$); (3) the same as (2) except that recruitment to the fishery in the current and future years (i.e., progeny spawned in 1988 and thereafter) is stochastic with $\sigma_r = 0.65$ (similar to, e.g., Francis 1992; Cordue 1993; Punt et al. 1993a); (4) assuming that steepness = 0.95; (5) assuming that steepness = 0.5; (6) assuming an informative prior for steepness (Fig. 3).

The alternative harvest policies considered were constant quotas ranging from 150 to 400 kt per year. For the purpose of this illustration, only a few of the performance statistics used will be reported for each alternative policy (see Appendix III).

Results

Stock Assessment

In test 1, we evaluated the effect on posteriors of using noninformative and informative priors for q_1 (Fig. 3; Table 4). Under the noninformative prior, it is possible to exclude lower stock sizes (e.g., $B_{cur} < 600$ kt have very low probability) (Fig. 3). However, the posterior over higher stock sizes is relatively flat, indicating that the data contain little information about higher stock sizes. Using an informative prior for q_1 reduces uncertainty markedly. The marginals are more peaked reflecting reduced odds of larger stock sizes (Fig. 3). The SDs for B_0, B_{cur}, and B_{cur}/B_0 for the informative prior were 7, 18, and 11% smaller than those for the base case, respectively (Table 4). The expected values for B_0, B_{cur}, and B_{cur}/B_0 drop under the informative prior, i.e., they are 9, 14, and 7% smaller than those under the noninformative one (Table 4).

Assuming that recruitment is deterministic and that all input parameters, except B_0 and q, are fixed, considerably underestimates uncertainty with respect to the baseline case (Fig. 3, test 2). For example, the SDs for B_0, B_{cur}, and B_{cur}/B_0 were reduced by 13, 2, and 26% from base case values. Estimates of B_0, B_{cur}, and B_{cur}/B_0 reduced by 13, 13, and 3% (Table 4). The effect of assuming a low-information prior for M was to drastically increase uncertainty. SDs for B_0, B_{cur}, and B_{cur}/B_0 increased by 13, 54, and 84% (Table 4, test 3). The effect of assuming a low-information prior for σ_r was less pronounced. SDs in B_0, B_{cur}, and B_{cur}/B_0 increased by 7, 3, and 20% relative to the base case (Table 4, test 4).

The effect of using fixed values for M and σ_r was negligible: only slight changes in the marginal posteriors can be observed. For example, the expected value for B_0 was nearly the same as that under the base case. The SDs decreased, as might be expected by a removal of a source of variability, but only slightly, e.g., by 2% for B_0 (Table 4, test 5).

The results are slightly more optimistic if steepness is 0.95 rather than 0.75 and less optimistic if steepness is 0.5 (Table 4, tests 6 and 7). For example, the estimate of B_{cur}/B_0 increases by 2% for h = 0.95 and decreases by 4% for h = 0.5. The effect of using the informative and noninformative priors for h as opposed to a point prior is negligible (tests 8 and 9). The estimates of B_0, B_{cur}, and B_{cur}/B_0 and their SDs are very similar to the base case (Table 4). However, the effects of these alternative priors for h on estimates of the risks and rewards of alternative harvesting policies could be more substantial and are evaluated in the next section.

TABLE 6. Fishery risk by state of nature.

	B_0 (Mt)						
Statistics	0.6–1	1–1.4	1.4–1.8	1.8–2.2	2.2–2.6	2.6–3	
Probability	0.012	0.1728	0.3228	0.2414	0.1628	0.0882	Expected
150-kt constant quota	0.083	0.009	0.000	0.000	0.000	0.000	0.003
200-kt constant quota	0.433	0.157	0.014	0.003	0.000	0.000	0.038
250-kt constant quota	0.733	0.531	0.129	0.024	0.001	0.002	0.148
300-kt constant quota	0.983	0.825	0.419	0.107	0.015	0.002	0.318
350-kt constant quota	1.000	0.946	0.706	0.307	0.087	0.025	0.492
400-kt constant quota	1.000	0.984	0.890	0.547	0.240	0.063	0.646

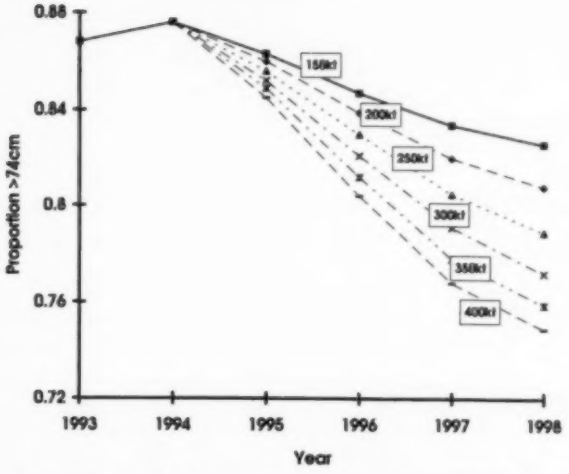


FIG. 4. Forecasts of the proportion of the catch greater than 74 cm (by number) given by the base case stock assessment.

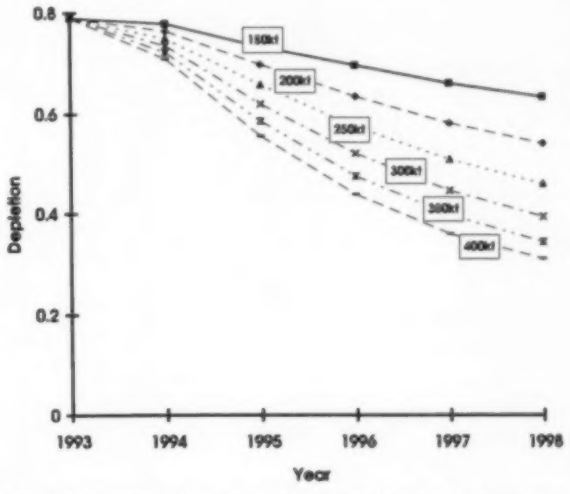


FIG. 5. Forecasts of the time series of midseason biomass as a fraction of its average pristine level given by the base case stock assessment.

Decision Analysis

The results of the decision analysis for the base case stock assessment are presented in the form of the expected values of the performance indices. Both average catch and risk increase as the size of the constant quota is increased (Table 5). As a result of increasing the quota, the lowest depletion and final stock size as a fraction of B_{MSY} are smaller. $P(B_{fin}/B_{MSY})$ and $E(B_{fin}/B_{MSY})$ are related almost linearly to expected catch size.

Fishery risk (the probability that catch will fall below 80% of the TAC in the next 5 yr) is largest for the lowest values of B_0 and risk as a function of B_0 drops off sharply with increasing B_0 (Table 6). The risks associated with low B_0 are substantially larger than the expected values of risk. This is because low B_0 is assigned a relatively low probability by the estimation procedure.

The estimates of the proportion of the catch that is marketable (i.e., larger than 74 cm) were of interest to industry because of drops in the fraction of market-sized fish in catches in recent years. The proportion of the market-sized individuals in the catch increases from 1993 to 1994 because of the effect of the large 1988 year-class, and then decreases. The rate at which this proportion decreases depends on the size of the expected catch, larger expected catches corresponding to larger declines (Fig. 4). The depletion time series shows a declining trend throughout the entire 1993–98 time period and for all the harvest policies considered (Fig. 5). This is to be expected, as the resource is currently well above B_{MSY}. Not surprisingly, the rate of reduction in biomass is largest for the largest expected catches.

In the first sensitivity analysis, we evaluated the effect on decision analysis results of using either informative or noninformative priors for the acoustic q (Fig. 6). Expected average catches are only slightly larger for the noninformative prior. Yet, for both priors, expected catches fall short of the quota as the quota increases (Fig. 6a). However, stock risk was approximately 35% higher for all of the policies evaluated using the informative prior (Fig. 6b). The index of catch variability used is "catch loss" (Appendix III) which indicates the expected size of a decrease in catch when one occurs. This measure of catch variability is more readily appreciated by industry members (for whom catch variability matters most) than the CV in catches which has been presented in other works (e.g., Bergh and Butterworth 1987). Catch loss is slightly larger in magnitude for the informative prior (2–5 kt larger for most policies) (Fig. 6c).

In the second sensitivity analysis, we evaluated the effects on decision analysis results of assuming that recruitment is either stochastic or deterministic (Fig. 7). Average catches are relatively insensitive to these assumptions (Fig. 7a). In contrast, stock risk is highly sensitive (Fig. 7b). If historic and future recruitments are assumed to be deterministic, the expected stock risks are about 30–40% of those under fully

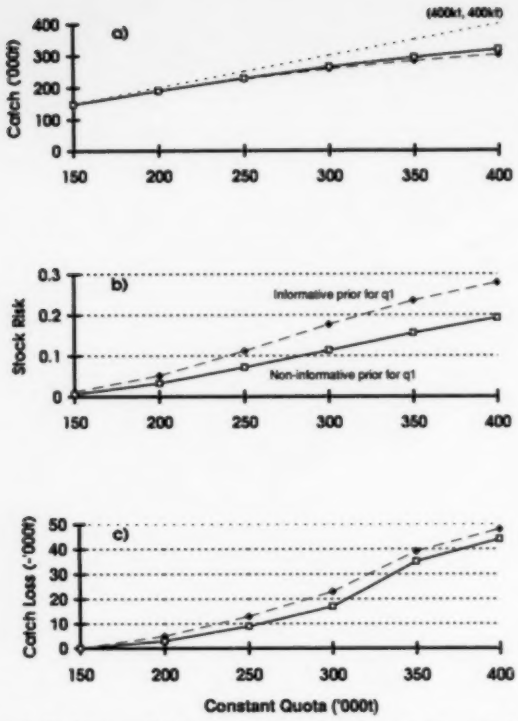


FIG. 6. Estimates of (a) catch, (b) stock risk, and (c) catch loss under the informative and noninformative priors for the acoustic q (see Appendix III for definitions).

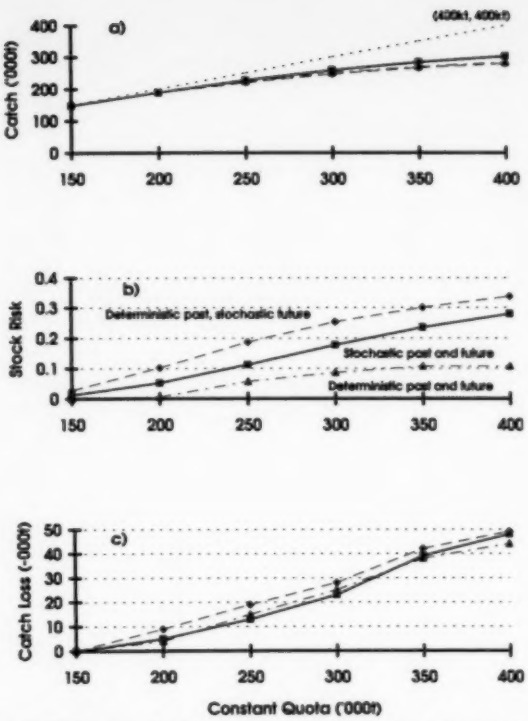


FIG. 7. Estimates of (a) catch, (b) stock risk, and (c) catch loss under assumptions that historic and future recruitment are deterministic, historic recruitment is deterministic but future recruitment is stochastic, and both historic and future recruitment are stochastic (see Appendix III for definitions).

stochastic recruitment (base case). However, if it is assumed that historic recruitment is deterministic but recruitment to the fishery in the current and future years is stochastic, then risks are as much as 50% higher than the base case (Fig. 7b). Catch loss is slightly larger (2–6 kt) in magnitude than the base case under the deterministic–stochastic scenario but very similar to the base case under the fully deterministic scenario (Fig. 7c).

Third, we evaluated the sensitivity of decision analysis results to different assumptions about steepness (h) (Fig. 8). Expected catches are very similar under the various assumptions (Fig. 8a). However, the assumption that $h = 0.5$ results in stock risks for some policies over 50% larger than risks given under all of the other assumptions (Fig. 8b). Assuming an informative prior results in stock risks that are intermediate between the assumptions that $h = 0.75$ and $h = 0.95$. The assumption that $h = 0.5$ results in estimates of catch loss that are slightly (2–6 kt) larger in magnitude than estimates given by all of the other assumptions (Fig. 8c).

Discussion

Several methods for estimating the risks and rewards of alternative harvesting policies already exist (e.g., Bergh and Butterworth 1987; Sainsbury 1988; Collie and Walters 1991; Francis et al. 1992; Restrepo et al. 1992, 1993; Walters and Punt 1994). This paper extends the use of the SIR algorithm to a Bayesian decision analysis of alternative harvesting policies. The SIR algorithm provides considerable versatility in dealing with problems in fisheries assessment (see Table 7 for a comparison of the Bayesian method in this paper with that in others). It can incorporate uncertainty in any number of parameters by incorporating them in a joint prior pdf. The algorithm can incorporate process error, for example, in the form of recruitment stochasticity. The algorithm can use a wide variety of data, both age-structured and non-age-structured data and data for the same and related species: These can be used either in the likelihood function or in developing informative priors. The algorithm can incorporate alternative population dynamics models and likelihood functions. It can evaluate both variable or constant catch quota policies and, with some modification, harvest rate policies that use future data on relative abundance (see below). It can evaluate both short- and long-term horizons. It can also evaluate almost any policy performance indicator that is of interest. Because of its versatility and intuitive appeal, the SIR algorithm, as applied in this paper, serves as a useful framework for facilitating the participation of industry members in harvest policy decisions, as has been our experience in applying the approach in New Zealand's orange roughy (Punt 1993) and hoki fisheries (Punt et al. 1993b, 1994). New applications of the algorithm are currently being developed in the Pacific northwest (e.g., Stocker et al. 1994).

Alternative Monte Carlo approaches for estimating multidimensional posteriors in Bayesian fisheries assessments include adaptive importance sampling (AIS) and Markov Chain Monte Carlo (MCMC) methods (Givens 1993a, 1993b;

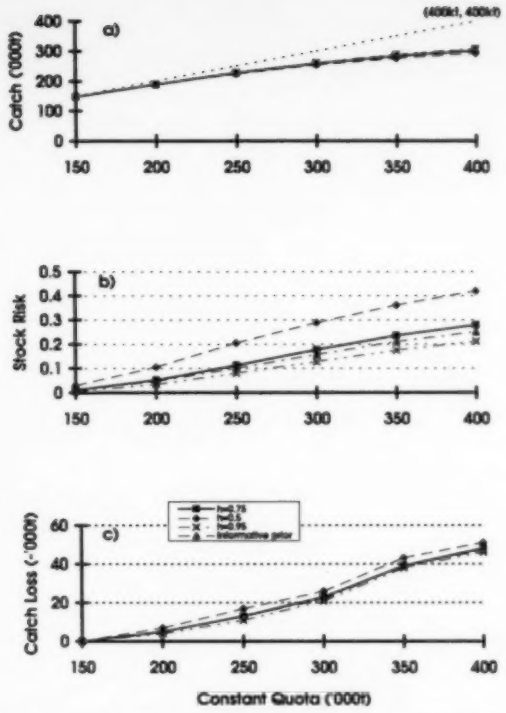


FIG. 8. Estimates of (a) catch, (b) stock risk, and (c) catch loss under the assumptions that steepness (h) in the Beverton–Holt stock–recruitment relationship is equal to 0.5, 0.75, and 0.95 or has the prior pdf shown in Fig. 2b.

Kinas 1993). In contrast with SIR, AIS is an iterative importance sampling procedure that uses as the importance function a finite mixture of multivariate pdfs, such as the multivariate Student density (Kinas 1993; West 1993). The normalized importance ratios are used to develop the new importance function, and successive rounds of importance sampling are conducted such that the successive importance functions converge on the posterior. A potential advantage of AIS over SIR is that AIS may be computationally more efficient than SIR, especially for estimating highly complex (e.g., multimodal), multidimensional posteriors (Kinas 1993). In contrast, MCMC methods, which consist of iterative Markovian updating schemes for estimating posteriors, may be computationally less efficient than importance sampling approaches (Smith 1991; Givens 1993a).

Evaluating Feedback Harvesting Policies with Monte Carlo Bayesian Methods

In the example provided, a more realistic problem would have been to evaluate alternative harvest rate policies rather than constant quota policies only. Data obtained in the future will almost certainly be used to update TACs. However, evaluation of such policies is complicated because it requires the simulation of future stock assessments. It is impractical to simulate the Monte Carlo assessment procedure because of computational demands.

Evaluation of alternative feedback harvest rate policies is made possible by simplifying future assessments. For example, Punt et al. (1993b) evaluated such policies by

TABLE 7. Comparison of six studies describing Bayesian approaches to fishery management.

Feature	Bergh and Butterworth (1987)	Thompson (1992)	Givens et al. (1993)	Hilborn et al. (1994)	Walters and Punt (1994)	This study
Population dynamics model	Age structured with linear-threshold recruitment	Simple dynamic pool (biomass dynamic) with Cushing recruitment	Sex and age structured with density-dependent calving rates	Sex and age structured with Beverton–Holt recruitment	Age structured but no explicit stock–recruit function	Sex and age structured with Beverton–Holt recruitment
Recruitment stochastic	Yes	No	No	No	Yes	Yes
Data used	Age-structured survey biomass as absolute indices	Stock and recruit	Non-age-structured population counts	Survey biomass as absolute indices	Catch-at-age and survey biomass as absolute indices	Survey and commercial fishery as relative indices of abundance
Number of uncertain parameters	8	3	8	1	2	48
Form of integration	Monte Carlo	Analytic	SIR algorithm	Numeric grid	Numeric grid	SIR algorithm
Time horizon	20-yr	Long-term	Current-year	10-yr	Next-year	Current-year and 5-yr
Policies evaluated	Harvest rate, constant escapement, and constant quota	Fishing mortality rate	None; replacement yield in the current year is estimated	Constant quota	This year's catch quota	Constant quota and harvest rate

simulating future assessments that used a grid-based Bayesian estimator. This estimator was fitted to the historic abundance indices and ones generated with random error in the current and future years. The estimator assumed that recruitment is deterministically related to spawner stock size and that, except for B_0 and the constants of proportionality for relative abundance indices, all other input values are known without error. For the same level of risk, harvest rate policies that were allowed to change by no more than 25% per year provided average catches 10–15% higher than those for constant quota policies. However, the harvest rate policies could be expected to result in net changes in catch up to 20% of the TACs, compared with only 13% for constant quota policies with similar average catches.

Including Process Error in Fisheries Stock Assessment and Decision Analysis

Several fisheries risk assessment methods assume that density-dependent processes are deterministic when their population dynamics models are fit to historic data (e.g., Sainsbury 1988; Francis 1992; Thompson 1992; Punt et al. 1993b; Hilborn et al. 1994). The example in this study, which incorporated recruitment stochasticity, indicates that such assumptions can lead to dramatic underestimates of uncertainty, and virgin and current stock size. These observations are qualitatively consistent with those in Francis et al. (1992) who also compared deterministic and stochastic recruitment assumptions in assessments of the Chatham Rise stock of orange roughy.

Policy choice can be strongly impacted by whether process error is incorporated in the assessment. For hoki, the forecasted risks of alternative harvesting policies decrease and larger constant quotas become more acceptable when the stochastic assumption for recruitment is replaced with the deterministic one. In contrast, when only historic recruitments are deterministic, and future recruitments stochastic, forecasted risks increase and make larger constant quotas much less desirable. This latter result is qualitatively consistent with the difference in risk estimates in Francis (1992) and Francis et al. (1992). The assumption that both historic and future recruitments are stochastic is the most compelling, and should replace deterministic assumptions whenever feasible in order to avoid potential large biases in estimates of stock status, uncertainty, and risk.

Use of Priors in Fisheries Stock Assessment and Decision Analysis

The example in this paper uses a prior pdf that assumes that all parameters are independent. This is a convenient shortcut to developing and implementing a joint prior pdf in the SIR algorithm and has been used in other fisheries applications (Givens et al. 1993; Kinas 1993; Punt 1993). A more sophisticated prior could account for expected correlations among parameters such as for B_0 and steepness (h), and B_0 and natural mortality rate (M). Note that such correlations are not to be confused with covariances in parameter estimates after the data have been fitted. Instead, these correlations should reflect what one would expect to find in nature. For example, from life history theory, a population with a high intrinsic rate of increase could be expected to also have a high rate of natural morality. Incorporating such correlations in a joint prior would be a useful step toward reducing uncertainty because unlikely combinations of parameter values would be given less weight in the prior. However, the task of incorporating correlations among parameters in a prior can be technically challenging because it requires the development of a suitable multivariate pdf of possibly very different types of parameters (e.g., M, h, and B_0) (see Kinas 1993). Furthermore, if the joint prior was strongly biased, more data would be needed before the posterior converged about the correct parameter values than if independence had been assumed.

The Bayesian approach enables analysts to draw from a broad spectrum of information and experience to construct informative priors. In the example, we applied an informative prior for the constant of proportionality for acoustic indices (q_1) that was constructed using Monte Carlo simulation of the sources of uncertainty in q_1. This approach can be used to construct informative priors for constants of proportionality for survey indices of abundance in other fisheries. The approaches that were used to construct informative priors for recruitment variability (σ_r) and steepness (h) can potentially help in constructing informative priors for parameters such as natural mortality rate, and other stock–recruit parameters. A refinement, however, would be to give the stocks that are the most dissimilar (e.g., in life history and environment) to the one under consideration less weight in the resulting pdf as suggested by Thompson (1992), rather than equal weight as in this study. By using informative priors for such quantities, uncertainty in Bayesian estimates of current stock size and stock–recruit parameters can be reduced considerably, as shown for hoki. Strict quality control, however, is needed in constructing informative priors because of the strong impacts on inference, and, ultimately, on policy choice that priors can have when data are relatively uninformative, as they are in most fisheries.

The example also shows that the use of noninformative priors as reference priors can help to reveal the relative importance of the data versus informative priors in reducing uncertainty for quantities of interest, and the relative importance of the various sources of uncertainty (Box and Tiao 1973). For hoki, the uncertainty in values for the constants of proportionality for relative abundance indices and M were very important relative to others. Assuming informative priors for these quantities helped considerably to reduce uncertainty in model output, resulted in higher forecasted risks, and made larger constant quota policies less acceptable. Assuming a variety of priors for other model quantities (e.g., h and σ_r) made much less difference in stock assessment results. However, in other situations, for example, where stock rebuilding from depleted conditions is of interest, uncertainties in h and σ_r may play a more important role.

In contrast, the alternative point priors for h gave considerably different estimates of risk for the various harvest options evaluated for hoki. This outcome is problematic because a decision must be made about which set of results to believe. The use of the informative prior for h eliminates this problem by effectively integrating the results from all potential individual sensitivity tests for alternative point values for h into a single result. Alternatively, the consequences of alternative policies under alternative values for such a parameter can be readily communicated by binning the decision analysis results over the parameter space of interest (e.g., as for B_0 in Table 6). The replacement of point priors by distribution-based priors thereby can make the calculation and presentation of results from stock assessment

and decision analysis more efficient by eliminating the need for cumbersome sensitivity tests that use different point values for various parameters (as in, e.g., Punt et al. 1993a). However, in Bayesian analysis, tests of the sensitivity of results to alternative prior pdfs often cannot be avoided.

The prior chosen for B_0 for hoki ($U(0, 3000$ kt)) could be refined. Punt et al. (1994) evaluated a variety of other priors for B_0 for hoki and found that decreases in the upper cut-off point at 3000 kt had more impact on decision-analysis results than increases. Other formulations such as uniform over $\log(B_0)$ or uniform over the amount of depletion from unexploited conditions but using the same range (0, 3000 kt) gave slightly more pessimistic results.

Interpreting the Results of Fisheries Decision Analysis

Lastly, the results of fisheries decision analysis are to be interpreted as forecasts, not predictions, since many future events that can effect a fishery are unpredictable (e.g., oceanographic anomalies, abrupt changes in the abundance of prey species, competitors, or predators, and market crashes). By associating probabilities with the potential consequences of each harvesting option, Bayesian decision analysis provides analysts with a powerful tool to convey such uncertainties to decision makers (Hilborn et al. 1993). Furthermore, the results of decision analysis can allow decision makers to use objective and quantitative criteria to make choices among progressively more optimistic policy options that entail trade-offs between risk and opportunity (Walters and Ludwig 1994). Bayesian decision analysis can thereby enable decision makers to deal with uncertainty in a more objective, rational manner.

Acknowledgments

This work was funded by the New Zealand Fishing Industry Board. We thank Patrick Cordue, Chris Francis, and Paul Starr for their critiques of the procedure. We also thank Geof Givens, Tim Hammond, Antonio Perez-Comas, Geir Oddsson, Beth Babcock, John Wallace, Steve Hare, Ana Parma, Tom Wainwright, Steve Mathews, Don Gunderson, and Pat Sullivan for their suggestions to improve earlier versions of the paper. Four anonomous referees are also thanked for their comments that helped to improve the presentation of the work. Kevin Sullivan and Patrick Cordue are thanked for providing data for hoki. We are grateful to Nick Barrowman and Ransom Myers for providing us with the stock and recruitment data for gadoids.

References

Berger, J.O. 1985. Statistical decision theory and Bayesian analysis. 2nd ed. Springer-Verlag, New York, N.Y. 617 p.

Bergh, M.O., and D.S. Butterworth. 1987. Towards rational harvesting of the South African anchovy considering survey imprecision and recruitment variability. S. Afr. J. Mar. Sci. 5: 937–951.

Bernardo, J.M. 1979. Reference posterior distributions for Bayesian inference. J.R. Stat. Soc. B 41(2): 113–147.

Box, G.E.P., and G.C. Tiao. 1973. Bayesian inference in statistical analysis. Addison-Wesley, Reading, Mass. 588 p.

Collie, J.S., and C.J. Walters. 1991. Adaptive management of spatially replicated groundfish populations. Can. J. Fish. Aquat. Sci. 48: 1273–1284.

Cordue, P.L. 1993. Minimized integrated average mean square error approach to biomass and risk estimation. N.Z. Fish. Assess. Res. Doc. 93/1.

Cordue, P.L., and R.I.C.C. Francis. 1994. Accuracy and choice of risk estimation for fisheries assessment. Can. J. Fish. Aquat. Sci. 51: 817–829.

Cordue, P.L., M.K. McAllister, E.K. Pikitch, and K.J. Sullivan. 1992. Stock assessment of hoki. N.Z. Fish. Assess. Res. Doc. 92/10.

DeGroot, M.H. 1970. Optimal statistical decisions. McGraw-Hill. New York, N.Y. 489 p.

Francis, R.I.C.C. 1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. Can. J. Fish. Aquat. Sci. 49: 922–930.

Francis, R.I.C.C., D.A. Robertson, M.R. Clark, and R.P. Coburn. 1992. Assessment of the QMA 3B orange roughy fishery for the 1992/93 season. N.Z. Fish. Assess. Res. Doc. 92/4.

Givens, G.H. 1993a. Contribution to discussion on the meeting on "The Gibbs sampler and other Markov chain Monte Carlo methods". J.R. Stat. Soc. B 55: 75–76.

Givens, G.H. 1993b. A Bayesian framework and importance sampling methods for synthesizing multiple sources of evidence and uncertainties linked by a complex mechanistic model. Ph.D. thesis, Department of Statistics, University of Washington, Seattle, Wash.

Givens, G.H., J.E. Zeh, and A.E. Raftery. 1993. Assessment of the Bering–Chukchi–Beaufort seas stock of bowhead whales using the hitter–fitter model in a Bayesian synthesis framework. Int. Waling Comm. Doc. SC/45/ASI.

Hilborn, R., E.K. Pikitch, and R.C. Francis. 1993. Current trends in including risks and uncertainty in stock assessment and harvest decisions. Can. J. Fish. Aquat. Sci. 50: 874–880.

Hilborn, R., E.K. Pikitch, and M.K. McAllister. 1994. A Bayesian estimation and decision analysis for an age-structured model using biomass survey data. Fish. Res. 19: 17–30.

Hilborn, R., and C.J. Walters. 1992. Fisheries stock assessment. Choice, dynamics, and uncertainty. Chapman and Hall, New York, N.Y. 570 p.

Jeffreys, H. 1961. Theory of probability. 3rd ed. Clarendon Press, Oxford. 447 p.

Kinas, P.G. 1993. Bayesian statistics for fishery stock assessment and management. Ph.D. thesis, Department of Statistics, University of British Columbia, Vancouver, B.C.

Myers, R.A., W. Blanchard, and K.R. Thompson. 1990. Summary of north Atlantic fish recruitment 1942–1987. Can. Tech. Rep. Fish. Aquat. Sci. 1743: 108 p.

Myers, R.A., J. Bridson, and N.J. Barrowman. 1993. Summary of worldwide stock and recruitment data. Can. Tech. Rep. Fish. Aquat. Sci. 2024: 327 p.

Punt, A.E. 1993. The implications of some multiple stock hypotheses for Chatham Rise orange roughy. N.Z. Fish. Assess. Res. Doc. 93/16.

Punt, A.E., D.S. Butterworth, and A.J. Penney. 1993a. Stock assessment and risk analysis for the South Atlantic population of albacore (*Thunnus alalunga*). ICCAT Doc. SCRS/93/72.

Punt, A.E., M.K. McAllister, E.K. Pikitch, and R. Hilborn. 1994. Stock assessment and decision analysis for hoki (*Macruronus novaezelandiae*) for 1994. N.Z. Fish. Assess. Res. Doc. 94/13.

Punt, A.E., E.K. Pikitch, M.K. McAllister, and R. Hilborn. 1993b. Stock assessment and decision analysis for the western stock of hoki (*Macruronus novaezelandiae*) for 1993. N.Z. Fish. Assess. Res. Doc. 93/13.

Raiffa, H. 1968. Decision analysis. Introductory lectures on choices under uncretainty. Addison-Wesley, Reading, Mass. 309 p.

Restrepo, V.R., J.M. Hoenig, J.E. Powers, J.W.Baird, and S.C. Turner. 1992. A simple simulation approach to risk and cost analysis, with applications to swordfish and cod fisheries. Fish. Bull. U.S. 90: 736–748.

Restrepo, V.R., C.E. Porch, S.C. Turner, G.P. Scott, and A.A. Rosenberg. 1993. Combination of spawner–recruit, spawning biomass-per-recruit computations for the estimation of the long-term yield potential for west Atlantic bluefin tuna. ICATT Doc. SCRS/93/72.

Rubin, D.B. 1987. Comment on "The calculation of posterior distributions by data augmentation". J. Am. Stat. Assoc. 82: 543–546.

Rubin, D.B. 1988. Using the SIR algorithm to simulate posterior distributions, p. 385–402. *In* J.M. Bernardo, M.H. Degroot, D.V. Lindley, and A.M. Smith [ed.] Bayesian Statistics 3: Proceedings of the Third Valencia International Meeting, June 1–5, 1987. Clarendon Press, Oxford. 805 p.

Sainsbury, K.J. 1988. The ecological basis of multispecies fisheries and management of a demersal fishery in tropical Australia, p. 340–382. *In* J.A. Gulland, [ed.] Fish population dynamics. Wiley, New York, N.Y.

Silverman, B.W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, New York, N.Y. 175 p.

Smith, A.F.M. 1991. Bayesian computational methods. Philos. Trans. R. Soc. Lond. A 337: 369–386.

Stocker, M., C.M. Hand, and M.K. McAllister. 1994. Pacific cod. *In* M. Stocker [ed.] Groundfish stock assessment for the west coast of

Canada in 1993 and recommended yield options for 1994. Can. Tech. Rep. Fish. Aquat. Sci. 1975: 50–92.

SULLIVAN, K.J. 1994. A review of the 1991–92 hoki fishery and assessment of hoki stocks for 1993. N.Z. Fish. Assess. Res. Doc. 94/2.

THOMPSON, G.G. 1992. A Bayesian approach to management advice when stock–recruit parameters are uncertain. Fish. Bull. U.S. 90: 561–573.

WALTERS, C.J., AND D. LUDWIG. 1994. Calculation of Bayes posterior probability distributions for key population parameters: a simplified approach. Can. J. Fish. Aquat. Sci. 51: 713–722.

WALTERS, C.J., AND A.E. PUNT. 1994. Placing odds on sustainable catch using virtual population analysis and survey data. Can. J. Fish. Aquat. Sci. 51: 946–958.

WEST, M. 1993. Approximating posterior distributions with mixtures. J.R. Stat. Soc. B 55: 409–422.

Appendix I: Population Dynamics Model

The model specified in this appendix is age and sex structured, relates recruitment to spawner biomass by means of the Beverton–Holt stock–recruitment relationship, and allows for stochastic recruitment.

A. Resource Dynamics

The dynamics of animals of sex s, aged 2 and above, are governed by the equation

$$N^s_{y+1,a} = e^{-M^s}\{N^s_{y,a-1}\, e^{-F_y}(1-H_y) + U^s_{y,a-1}\tau^s_a\} \qquad 2 \le a < m$$

$$\text{(I.1)} \quad U^s_{y+1,a} = e^{-M^s} U^s_{y,a-1}(1-\tau^s_a) \qquad 2 \le a < m$$

$$N^s_{y+1,m} = e^{-(M^s+F_y)}(N^s_{y,m} + N^s_{y,m-1})(1-H_y) \qquad a = m$$

where $N^s_{y,a}$ is the number of recruited animals of age a and sex s at the start of year y, $U^s_{y,a}$ is the number of unrecruited animals of age a and sex s at the start of year y, τ^s_a is the proportion of unrecruited animals of age $a-1$ and sex s which recruit at age a:

$$\text{(I.2)} \quad \tau^s_a = (\phi^s_a - \phi^s_{a-1})/(1-\phi^s_{a-1}),$$

ϕ^s_a is the fraction of animals of age a and sex s which would be recruited if the population were at its deterministic unexploited equilibrium level, M^s is the instantaneous rate of natural mortality on animals of sex s, F_y is the fishing mortality during year y which results from the catches before the spawning season (all recruited animals are assumed to be equally vulnerable to fishing), H_y is the exploitation rate during the spawning season of year y, and m is the maximum (lumped) age-class (all animals in this and the previous age-class are recruited and mature).

B. Births

$$\text{(I.3)} \quad N^s_{y,1} = 0$$

$$U^s_{y,1} = 0.5[\mu B^s_{y-1}/(\alpha + \beta\mu B^s_{y-1})]e^{\epsilon_y - \sigma_r^2/2}$$

where B^s_y is the biomass of mature females during year y at the time of spawning:

$$\text{(I.4)} \quad B^s_y = \sum_{a=1}^{m} w^f_a e^{-(M^s+F_y)} N^f_{y,a}(1 - H_y/2)$$

μ is the proportion of the midseason mature biomass that spawn each year, w^s_a is the mass of a fish of sex s and age a (assumed to be constant throughout the year):

$$\text{(I.5)} \quad w^s_a = \delta^s_1 (L^s_a)^{\delta^s_2}$$

$$\text{(I.6)} \quad L^s_a = L^s_\infty (1 - e^{-\kappa^s(a-t^s_0)})$$

ϵ_y is the recruitment residual for year y, $\epsilon_y \sim N(r_y, \sigma_r^2)$ and it is assumed that $r_y = 0$, unless specified otherwise, $e^{\epsilon_y - \sigma_r^2/2}$ is referred to as the recruitment multiplier, σ_r is the standard deviation of the log of the multiplicative fluctuations in births, and α and β are stock–recruitment function parameters.

C. Initial Conditions

Were there no fluctuations in recruitment, the resource would be assumed to be at its unexploited equilibrium level, with the corresponding age structure, at the start of exploitation (year y_1). Instead, because of historic recruitment fluctuations, the sizes of the cohorts at the start of year y_1 are drawn from pdfs that allow for this fluctuation, and the initial biomass is thus similarly distributed about the corresponding deterministic equilibrium level. The initial numbers-at-age are given by the equation

$$N^s_{y_1,a} = 0.5R_1\phi^s_a \exp\{-(a-1)M^s\}e^{\epsilon_a - \sigma_r^2/2} \qquad 1 \le a \le m-1$$

$$\text{(I.7)} \quad N^s_{y_1,m} = 0.5R_1 \exp\{-(m-1)M^s\}/(1-\exp(M^s)) \qquad a = m$$

$$U^s_{y_1,a} = 0.5R_1(1-\phi^s_a)\exp\{-(a-1)M^s\}e^{\epsilon_a - \sigma_r^2/2} \qquad 1 \le a \le m-1$$

where R_1 is the number of 1-yr-olds at the deterministic equilibrium that corresponds to an absence of harvesting and ϵ_a is a random variable from $N(0,\sigma_r)$. A value for R_1 is calculated from the value for the virgin biomass at midyear, B_0, using the equation

$$R_1 = B_0 / 0.5 \sum_s \left\{ \sum_{a=1}^{m-1} w^s_a \phi^s_a \exp(-aM^s) + w^s_m \exp(-mM^s)/(1-\exp(-M^s)) \right\}$$

Note that the equation for the plus-group does not incorporate a recruitment variability term because this group comprises a large number of age-classes which will largely damp out this effect. Values for the stock–recruit parameters α and β are calculated from the values of R_1 and the "steepness" of the stock–recruit relationship (h). The "steepness" is the fraction of R_1 to be expected (in the absence of recruitment variability) when the mature biomass is reduced to 20% of its pristine level (Francis 1992), so that

$$\alpha = \mu \tilde{B}^S_0 \frac{1-h}{4h}$$

$$\text{(I.8)} \quad \beta = \frac{5h-1}{4hR_1}$$

$$\tilde{B}^S_0 = 0.5\left\{ \sum_{a=1}^{m-1} w^f_a \phi^f_a \exp(-aM^f) + w^f_m \exp(-mM^f)/(1-\exp(-M^f)) \right\}.$$

D. Catches for the Western Stock of Hoki

The exploitation rate during the spawning season of year y, H_y, is calculated using the equation

(I.9) $H_y = C_y^S / B_y^f$

where C_y^S is the spawning-season catch during year y and B_y^f is the exploitable biomass at the start of the spawning-season fishery in year y:

(I.10) $B_y^f = \sum_s \sum_a w_a^s N_{y,a}^s e^{-(M^s + F_y)}$.

The fishing mortality during year y which results from catches before the spawning season, F_y, is obtained by solving the equation

(I.11) $C_y^P + \sum_s \sum_a \frac{w_a^s F_y N_{y,a}^s (1 - e^{-(M^s + F_y)})}{M^s + F_y}$

where C_y^P is the catch taken during year y before the spawning season. Cordue et al. (1992) defined the maximum possible exploitation rate for west coast hoki during the spawning season by means of the equation

(I.12) $H_{crit} = \frac{\mu\varphi\bar{p}_j}{1 - 0.5\varphi(1 - \bar{p}_j)}$

where $\bar{p}_j$ is the average proportion of the spawning biomass in the area open to fishing in year j and φ is the maximum catch to spawning biomass ratio (i.e., set for $\bar{p}_j = 1$).

E. Data Series for the Western Stock of Hoki

The acoustic data are assumed to be proportional to midseason spawner biomass (i.e., μB_y^S). The trawl survey data are assumed to be proportional to the mature biomass of all 4+ fish after the spawning season, and the CPUE data are assumed to be proportional to the product of the annual proportion outside the 25 nautical mile limit and the midseason spawner biomass (i.e., $\bar{p}_y \mu B_y^S$).

Appendix II: Likelihood Function

All series of abundance indices are treated as being normally distributed about their expected values with a constant (and known) CV, i.e.,

(II.1) $O_j^i = q^i G_j^i + \eta_j^i \qquad \eta_j^i \sim N[0, (c_j^i q^i G_j^i)^2]$

where O_j^i is the jth value of the ith series, q^i is the constant of proportionality of the ith series, G_j^i is the model estimate of the quantity corresponding to O_j^i (e.g., the midseason spawner biomass for the acoustic indices), and c_j^i is the CV for the jth index of series i.

Francis et al. (1992) showed that the contribution of index i to the log-likelihood is

(II.2) $\lambda^i = -0.5 n^i \log(2\pi) - \sum_j \log(c_j^i G_j^i) - n^i \log(q^i)$

$$- 0.5 \sum_j [O_j^i / (q^i G_j^i) - 1]^2 / [c_j^i]^2$$

where n^i is the number of data points for abundance index series i.

Appendix III: Harvest Policy Performance Indices

Some of the performance indices used in the 1993 assessment of hoki are as follows. Risk (stock): the probability that (i.e., the proportion of projections in which) the biomass of mature fish (at midyear) drops below 20% of B_0 some time over the period 1993–98; Risk (fishery): the probability that the catch drops below 80% of the TAC some time over the period 1993–98; Catch: the average annual catch biomass over the period 1993–98; $E(B_{fin}/B_{MSY})$: the mean of the ratio of the midseason biomass at the end of the projection period to the midseason biomass corresponding to MSY (note that B_{MSY} differs from projection to projection because M changes from projection to projection); $P(B_{fin} > B_{MSY})$: the probability that the midseason biomass at the end of the projection period is larger than the midseason biomass at which MSY is achieved; Catch loss: the mean size of a drop in catch given that there is a drop in catch.

Fishing Tactics in a Two-Species Fisheries Model: The Bioeconomics of Bycatch and Discarding

David B. Sampson

Oregon State University, Coastal Oregon Marine Experiment Station, Hatfield Marine Science Center, Newport, OR 97365, USA

Sampson, D.B. 1994. Fishing tactics in a two-species fisheries model: the bioeconomics of bycatch and discarding. Can. J. Fish. Aquat. Sci. 51: 2688–2694.

The selections for fishing location largely determine the species mix and value of a fisher's catch. Because of travel costs, these choices also determine the profitability of a fishing trip. This paper develops a simple theoretical model for the selection of fishing locations by a fisher faced with two co-occurring species whose densities vary with distance from port. For each species there can be different catchability coefficients, handling times, and prices. The duration of each fishing trip is assumed fixed. The model is used to determine the profit-maximizing fishing tactics (the fishing locations and time spent at each location) and to explore the conditions that generate deliberate bycatch and discarding when one of the species cannot be sold because it is unmarketable or because of trip limits.

Le choix d'un lieu de pêche joue un rôle déterminant dans la composition spécifique et la valeur des prises d'un pêcheur. À cause des coûts de déplacement, ce choix détermine aussi la rentabilité d'une campagne de pêche. J'ai élaboré un modèle théorique simple permettant à un pêcheur de choisir entre des lieux de pêche lorsqu'il se trouve devant deux espèces co-occurrentes dont la densité varie avec la distance du port. On peut observer entre les espèces des différences dans le coefficient de capturabilité, le temps de manutention et le prix. On pose que la durée de chaque campagne est fixe. Le modèle sert à déterminer les tactiques de pêche les plus rentables (lieux de pêche et temps passé à chaque endroit) et à examiner les conditions qui génèrent des prises accessoires et des rejets délibérés quand une des espèces ne peut pas être vendue parce qu'elle ne répond pas aux conditions du marché ou à cause des limites de prises par sortie.

Received February 4, 1994
Accepted October 4, 1994
(J12261)

Reçu le 14 février 1994
Accepté le 4 octobre 1994

Fisheries scientists spend considerable time and money studying fish: how many there are, how long they live, how fast they grow and reproduce, and how they respond to changing environmental conditions. By comparison, fisheries scientists devote very little time and money to the study of fishers and their behavior. Yet it is the fishers that the management agencies regulate; the fish stocks are only affected indirectly, if at all. If fisheries management policies are to be fully effective and successful, then managers must be able to anticipate how fishers will respond to regulations, lest those regulations produce undesired outcomes. In this paper, I develop a simple model for one aspect of fishers' behavior, their choice of fishing locations; I use the model to analyze how fishers would modify their behavior in response to "trip limits", which are legal or market restraints on a boat's landings per trip.

The Pacific Fishery Management Council uses trip limits as a management device to slow the pace of certain fisheries along the U.S. Pacific coast and thereby extend the fishing season through the entire year (Pacific Fishery Management Council 1993). Trip limits have also been used in regulating groundfish fisheries in New England (Anthony 1990) and on the west coast of Canada (Tyler 1988). Under this form of regulation, when a boat makes a tow that causes its cumulative catch to exceed the legal trip limit, the excess fish must be discarded at sea. Boats landing more than the limit are subject to fines. Fishers claim that trip limits result in the discarding of significant amounts of marketable fish. For example, Pikitch et al. (1988) reported observing that between 12 and 16% of the catches of widow rockfish (*Sebastes entomelas*) were discarded at sea.

It is not just management agencies that restrict how much fish the fishers can bring to shore. Sometimes the fish processors and dealers to whom the fishers sell their catch impose "market limits" on the amount of fish they will buy per delivery (Pikitch et al. 1988).

Although making direct observations of fishers is probably the best approach to studying their behavior, the process is both time-consuming and costly. In this work, I develop a theoretical model of fishers' behavior that might provide some guidance for the design of future investigations, either empirical or theoretical. The model is based on numerous simplifying assumptions. Of particular note are the assumptions that the fish distributions are well defined and static over the course of a fishing trip and that a fisher has perfect knowledge of the catch rates he or she will experience while fishing at any location. Another major premise is that the primary short-run response available to fishers is their choice of fishing location. I assume that over the short time span of a fishing trip (days or weeks), fishers cannot easily change their boats or gear. Finally, I assume that fishers conduct their fishing operations in the manner that will maximize their profits. In choosing where to fish, they consider not only the species mix and catch rates they are likely to make at different fishing spots, but also the costs that arise from fishing there.

In this paper, I extend the basic model of Sampson (1991), which analyzed an unregulated fisher's choice of fishing location when harvesting from a single fish stock. There are some other published works that include theoretical models of fishing location choice, but from the viewpoint of the spatial dynamics of a fleet as opposed to the tactics of an individual fisher. Mangel and Clark (1983) analyzed a model fishery in which a fleet exploits two independently fluctuating stocks that are spatially distinct; they showed that exploratory fishing to obtain information on the relative fish abundance in the two areas can lead to significantly increased catches. Allen and McGlade (1986) developed a stochastic simulation model that couples the population dynamics of several fish stocks with the movements of fishing vessels between fishing zones; they used their model to explore how fishers might respond to changing information about catch rates. Hilborn and Walters (1987) described a general framework for modeling the spatial dynamics of a fish stock and a fishing fleet, which they used to investigate the relationship between catch per unit effort and fish abundance.

There have also been some empirical studies of fishing location choice. Gulland (1955) reported a tendency for fishing effort for North Sea haddock to be concentrated in geographic regions where there was high catch per unit effort. Hilborn and Ledbetter (1979) examined the weekly fishing patterns of the salmon purse-seine fleet in British Columbia and concluded that vessels moved between fishing areas to take advantage of changing catch rates. Eales and Wilen (1986) came to a similar conclusion based on their analysis of the daily operations of shrimp trawlers off northern California.

Healey and Morris (1992) and Gillis et al. (1993) applied the "ideal free distribution" hypothesis from behavioral ecology (Fretwell 1972) in their studies of the spatial patterns of fishing. In the fisheries context, this model predicts that if fishers know the fish distributions and the locations and activities of competing fishers, and if they can move freely between areas, then the fish abundance and catch per unit effort will tend to become equalized over all areas. Note that this is a fleet-wide phenomenon; the model makes no predictions about the activities of any single fisher. Healey and Morris (1992) found that the distribution of salmon trollers off British Columbia generally conformed to an ideal free distribution. Gillis et al. (1993) also established support for the hypothesis in a study of the trawl fishery in Hecate Strait, British Columbia.

At least two published econometric studies explicitly recognize the influence of fishing location choice on the economic performance of fishers, but neither of these studies develop detailed microeconomic models for a fisher's behavior. In choosing the form and estimating parameter values for a production function for the Tasmanian rock lobster fishery, Campbell (1991) accounted for differences in catch rates between vessels fishing inshore versus offshore. In a study of the influence of price variability on the behavior of British Columbia salmon fishers, Dupont (1993) controled for several factors that potentially influence how the fishers distribute themselves over three fishing grounds.

In this study, I have two objectives: (1) to develop from first principles a general model for a fisher's selection of fishing tactics and examine the properties that emerge from the model and (2) to analyze the specific contention that the discard problem in some trawl fisheries is due to the restrictive trip limits under which the fishers must operate. It is not my intent that the model accurately describe the characteristics of any actual fishery. I believe that by studying a hypothetical fishery, such as the one presented here, one can better understand the processes at work in a real fishery.

Although the model in this paper is reasonably simple, it nevertheless involves numerous variables and parameters (Table1).

TABLE 1. Variables and parameters of the model.

D_A, D_B	Biomass density functions for species A and B
d	Distance from port
B_A, B_B	Stock biomass of species A and B
μ_A, μ_B	Locations of peak biomass density for species A and B
σ_A, σ_B	Spatical variability parameters for the biomass density of species A and B
C_A, C_B	Catch weights per trip of species A and B
q_A, q_B	Catchability coefficients for species A and B
T	Total duration of a fishing trip
tF, tH, ts	Time per trip spent fishing the gear, handling the catch, and steaming to and from the fishing grounds
h_A, h_B	Handling time per unit weight of the catch for species A and B
R	Skipper's revenue per trip
S	Skipper's share of the catch
p_A, p_B	Unit prices for species A and B
V	Speed (velocity) of the fishing boat while steaming
limit_A	Trip limit for species A
K	Total operating costs per trip
kE, kL, kM	Costs per trip for fuel (energy), labor, and miscellaneous expenditures
pE	Unit price for fuel
uS, uF, uH	Rates of fuel use while steaming, fishing the gear, and handling the catch
W	Wage rate
π	Skipper's profit per trip

Model for Choice of Fishing Location

The individual fish that constitute any fish stock are almost certainly distributed irregularly in time and space. Areas with high fish densities at one season can have low densities at other seasons, and the pattern can change from year to year. As a consequence, for any mathematical model of fish distributions to be fully realistic, it would almost certainly have to be very complicated. For simplicity in this paper, I assume that the fish distributions are stable, at least for the time it takes to plan and complete a fishing trip, and I collapse the spatial dimensions to a single dimension, distance from port (d). I consider the actions of a fishing boat operating exclusively from its home port.

Assume there are two commercially harvested species of fish, A and B, whose biomass densities are normally distributed with distance from port. The equation describing the density of species A at location d is given by

$$(1) \qquad D_A = \frac{B_A}{\sigma_A \cdot \sqrt{(2 \cdot \pi)}} \cdot \exp\left[\frac{-(d-\mu_A)^2}{2 \cdot \sigma_A^2}\right]$$

where B_A is essentially the total stock biomass of species A, μ_A controls the location of the peak biomass density of A,

and σ_A controls whether A is widely or narrowly spread. A similar equation describes the density of species B. Other than mathematical convenience, I have no basis for choosing a normal distribution to model the spatial density of the fish. In a real fishery the fish distributions will likely depend on a variety of factors including local bathymetry, bottom sediments, oceanographic conditions, and previous spatial patterns of fishing.

While a boat is fishing at a particular location, assume that the catches accumulate in proportion jointly to the fish densities (D_A and D_B) and the time spent deploying the gear (tF). Because the fish densities vary with d, the distance from port, the catches also depend on d. The equations describing the catches (C) of species A and B are given by

$$(2) \qquad \begin{aligned} C_A &= q_A \cdot D_A \cdot \mathrm{tF} \\ C_B &= q_B \cdot D_B \cdot \mathrm{tF}. \end{aligned}$$

Parameters q_A and q_B are the "catchability coefficients" for species A and B. They measure the ability of the fishing boat and gear to catch A and B and control the extent to which the fisher can selectively harvest one species when the two species co-occur. The model in this paper assumes that the fisher cannot alter q_A and q_B during a trip. When the fish densities are both unity, q_A and q_B are equivalent to the catch rates for A and B.

The fish that are caught and brought aboard the boat may require sorting before the gear can once again be deployed. Assume that each fish caught requires time for handling and processing and that no further catching can occur while the fish are being handled. The amount of time for handling and processing (tH) varies with the size of the catch and is given by

$$(3) \qquad \mathrm{tH} = h_A \cdot C_A + h_B \cdot C_B$$

where h_A and h_B are the amounts of time the crew must spend handling and processing unit quantities of A and B.

Often, fish dealers are supplied by numerous boats and the market for fish is too large to be affected by the landings of any single boat (Anderson 1986). In this case, it is reasonable to treat fish prices as constant and to model the gross revenue flow (R) to the skipper of a fishing boat by

$$(4) \qquad R = S \cdot (p_A \cdot C_A + p_B \cdot C_B)$$

where S is the fraction of the landed catch that the skipper receives as his share (Sutinen 1979) and p_A and p_B are the unit prices for A and B. When catches are relatively large and trip limits are binding, the gross revenue flow is restricted to the value of the trip limits.

When fish are landed fresh, rather than frozen, dealers often will not purchase fish that have been dead for more than a short time; the fishers schedule their fishing trips accordingly. For the model in this paper, assume that the total duration of a fishing trip (T) is fixed and comprises time spent steaming to and from the grounds (tS), time spent searching for fish and working the gear (tF), and time spent handling the catch (tH):

$$(5) \qquad T = \mathrm{tS} + \mathrm{tF} + \mathrm{tH}.$$

In a real fishery, these activities will overlap to some degree.

The steaming time required to travel to the fishing grounds and return is determined by the boat's speed (V) and the skipper's choice of fishing location (d):

$$(6) \qquad \mathrm{tS} = 2 \cdot d/V.$$

The time available for fishing is also determined by the skipper's choice of fishing location:

$$(7) \qquad \begin{aligned} \mathrm{tF} &= T - \mathrm{tS} - \mathrm{tH} \\ \mathrm{tF} &= \frac{T - 2 \cdot d/V}{1 + h_A \cdot q_A \cdot D_A + h_B \cdot q_B \cdot D_B}. \end{aligned}$$

The skipper's choice of where to fish determines the steaming time and the catch rates, which in turn fix the time for fishing and handling.

The skipper's gross revenue flow (eq. 4) can now be written as a function of the decision variable d. If there are no binding trip limits, then

$$(8a) \qquad R(d) = S \cdot [p_A \cdot q_A \cdot \mathrm{F} D_A(d) + p_B \cdot q_B \cdot D_B(d)] \cdot \mathrm{tF}(d).$$

If there is a binding trip limit on the landings of species A, for example, then

$$(8b) \qquad R(d) = S \cdot [p_A \cdot \mathrm{limit}_A + p_B \cdot q_B \cdot D_B(d) \cdot \mathrm{tF}(d)].$$

To determine which fishing location results in the maximum profit flow to the skipper, one must describe how operating costs vary with fishing location.

Assume that costs (K) during a fishing trip accrue for fuel (kE), labor (kL), and other miscellaneous (kM) expenditures:

$$(9) \qquad \begin{aligned} K &= \mathrm{kE} + \mathrm{kL} + \mathrm{kM} \\ K &= \mathrm{pE} \cdot (\mathrm{uS} \cdot \mathrm{tS} + \mathrm{uF} \cdot \mathrm{tF} + \mathrm{uH} \cdot \mathrm{tH}) + W \cdot T + \mathrm{kM} \end{aligned}$$

where pE is the unit price for fuel (energy), uS, uF, and uH are the rates of fuel consumption while steaming, fishing, and handling, respectively, and W is the wage rate (if any) for the crew. These operating costs are the cash expenditures for the fishing trip. They do not include any "fixed costs", such as insurance, license fees, and interest payments, which accrue even when the boat remains at the dock. For simplicity, assume that no fuel is consumed while the catch is being handled, i.e., uH = 0. The skipper's cost flow (eq. 9) can now be written as a function of the decision variable d:

$$(10) \qquad K(d) = \mathrm{pE} \cdot [\mathrm{uS} \cdot 2 \cdot d/V + \mathrm{uF} \cdot \mathrm{tF}(d)] + W \cdot T + \mathrm{kM}.$$

The profit flow to the skipper is just the difference between the revenue and cost flows:

$$(11) \qquad \pi(d) = R(d) - K(d).$$

Given values for the biological parameters (B_A, μ_A, σ_A, B_B, μ_B, σ_B), economic parameters (S, p_A, p_B, pE, W, kM), technical parameters (q_A, h_A, q_B, h_B, V, uS, uF, uH), and constraints (T, limit_A) and given the assumption that a skipper operates to maximize his profits, one can use the profit flow equation to determine the fishing location that maximizes profit flow and to explore how profit flow and the choice of fishing location depend on the various characteristics of the fishery, such as the separation between species A and B, the relative prices for the two species, the technical characteristics of the boat and gear, or the management regulations.

Let d^* represent the value of d that maximizes $\pi(d)$. If the revenue and cost functions are continuous functions of d, then d^* will satisfy the condition $R'(d^*) = K'(d^*)$, where R' and K' are the partial derivatives of the revenue and cost functions with respect to the decision variable d. However, if there is a binding trip limit, the revenue function is not continuous and the maximum profit flow can occur at a discontinuity. Because of this complication, I was unable to derive an analytical solution for d^*. Instead, I used simple numerical techniques to solve for d^* for particular sets of parameter values (Table 2).

TABLE 2. Parameter values used to generate the figures (mt = metric tons).

	Fig. 1	Fig. 2	Fig. 4	Fig. 5
Biological parameters				
B_A (mt)	3000	3000	3000	3000
μ_A (km)	30	45	30	30
σ_A (km)	10	10	10	10
B_B (mt)	3000	3000	3000	3000
μ_B (km)	70	55	70	70
σ_B (km)	10	10	10	10
Economic parameters				
S (%)	30	30	30	30
p_A ($/mt)	6.0	6.0	10.0	10.0
p_B ($/mt)	12.0	12.0	12.0	12.0
pE ($/l)	1.0	1.0	1.0	1.0
W ($/hr)	1.0	1.0	1.0	1.0
kM ($)	0.0	0.0	0.0	0.0
Technical parameters				
q_A (1/h)	0.020	0.020	0.020	0.020
h_A (h)	0.50	0.50	0.50	0.50
q_B (1/h)	0.020	0.020	0.020	0.020
h_B (h)	0.50	0.50	0.50	0.50
V (km/h)	8.0	8.0	8.0	8.0
uS (l/h)	1.0	1.0	1.0	1.0
uF (l/h)	2.0	2.0	2.0	2.0
T (h)	24.0	24.0	24.0	24.0
limit_A (mt)	5.0	5.0	10.0	5.0

Results

Figure 1 illustrates a situation in which species A and B are well separated on the fishing grounds. Because their spatial distributions have little overlap (top panel), the fisher can "target" on one species by an appropriate choice of fishing location. The middle panel shows how revenues per trip (the solid line) and costs per trip (the dashed line) vary with distance from port when there is a binding trip limit on landings of species A. The flat section of the revenue curve (left of center) represents fishing locations that produce catches of A that exceed the trip limit. The "dash–dot" curve shows the revenue that results when there is no binding trip limit. The vertical dotted line on the right represents the "optimum" distance from port, the location that produces the maximum profit flow. The vertical dotted line on the left shows the optimum distance when there is no binding trip limit.

The bottom panel of Fig. 1 depicts the catches per trip from fishing at each location, the catch of A by the solid line and the catch of B by the dashed line. When the trip limit on species A is binding, the catch at the optimum fishing location is composed almost exclusively of species B. Locations that produce large catches of A result in large discards (the dotted line) and are unprofitable. However, when the trip limit on A is not binding, the catch at the optimum location consists almost exclusively of A.

When the two species are almost totally coincident on the fishing grounds (Fig. 2), it is essentially impossible to catch species A without also catching species B, and the binding trip limit on A has only a small effect on the optimum fishing location. However, fishing at the optimum location yields a substantial catch of species A, much of which is discarded because of the trip limit.

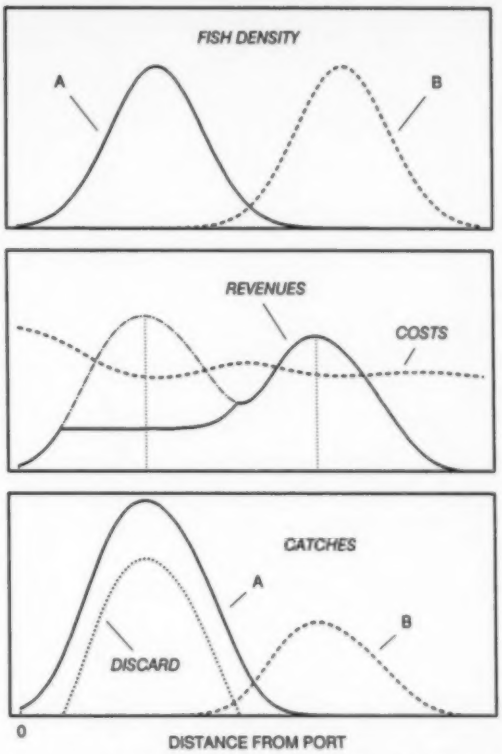


FIG. 1. A boat operates from a single port and fishes on two well-separated fish stocks (top panel). The revenues per trip and costs per trip (middle panel) vary with the skipper's choice of fishing location. A binding trip limit on the landings of species A distorts the revenue curve (middle panel, dash–dot line). The fisher operates further from port (middle panel, rightmost vertical dotted line) and the catch is composed primarily of species B (bottom panel).

Except for changing μ_A and μ_B to shift the locations of the fish distributions, I used identical parameters (Table 2) to generate Figs. 1 and 2.

The negative slope to the cost functions in these figures results from uS being less than uF; fuel consumption is less while steaming to and from the grounds than it is while fishing the gear. This condition could exist in a trawl fishery, for example, if a trawler had to apply extra power to overcome the drag of the net. When uF is less than uS, as might occur in a longline or gillnet fishery, costs increase with distance from port. The curvature in the cost functions is due to the positive handling times (h_A and h_B both greater than zero) and the diminished rate of fuel consumption during fish handling (uH = 0).

In Fig. 1, where the two stocks are widely separated, the imposition of the trip limit on landings of species A does not result in any discarding of A because the fisher radically alters tactics and fishes where species B is concentrated. However, if the trip limit is less restrictive, then some discarding could occur (Fig. 3). If the stocks are almost coincident (Fig. 2), then it seems that the fraction of the catch of A that is discarded varies linearly with the size of the trip limit (Fig. 3). Once the trip limit becomes binding, any further reductions in the limit result in increased discarding.

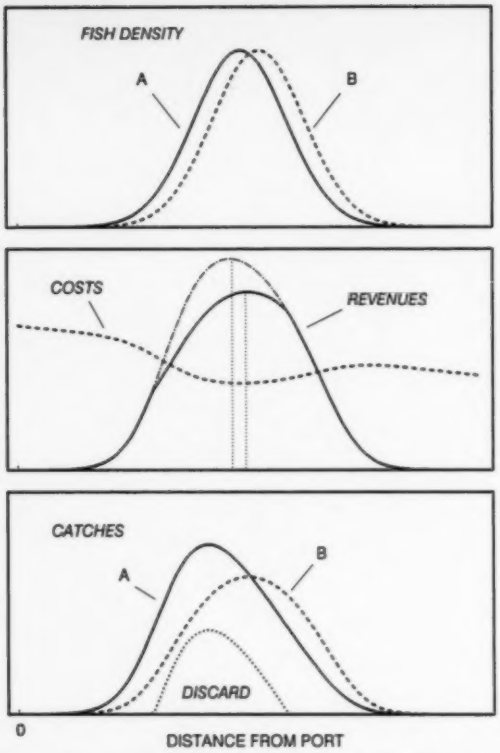


FIG. 2. A boat operates from a single port and fishes on two overlapping fish stocks (top panel). In this case the binding trip limit on A has little effect on the optimum fishing location (middle panel, vertical dotted lines). The fisher cannot avoid making an incidental bycatch of A, most of which is discarded (bottom panel, dotted line).

Given a trip limit of zero, which represents a complete ban against landing any of species A, the fisher continues to catch some of A, but all of it is discarded. However, if the stocks are distinct, the ban on landing species A results in no catches or discards of A.

Extension for Multiple Fishing Locations

The model above assumes that the skipper selects only one fishing location during a trip. However, when trip limits apply, the best fishing strategy might be to fish at more than one location, e.g., fish at one site to catch the limit of species A and then move and fish elsewhere to finish the trip with catches of species B. One can use the following approach to investigate whether fishing at two locations could produce greater profits than fishing at the best single location.

Let d_1 denote the first fishing location and let tF_1 denote the time spent fishing there. Because the total trip duration is fixed, feasible locations for a second fishing site (d_2) and the time available for fishing there (tF_2) are limited by the skipper's choice for d_1 and tF_1. Sites closer to port than the first are always feasible because they require no additional steaming time beyond what was required to reach the first site. However, sites that are further from port require additional

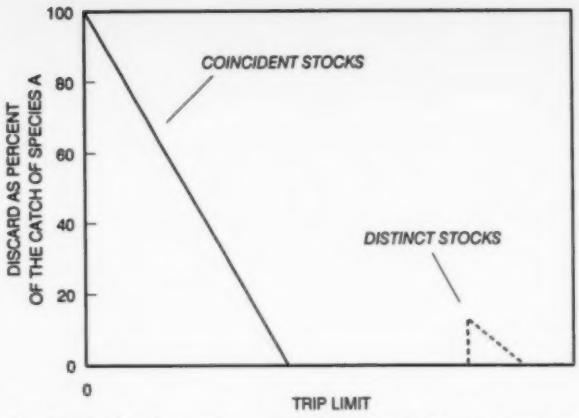


FIG. 3. The fraction of the catch of species A that is discarded depends on the size of the trip limit and on the degree of separation between the fish stocks.

steaming time; d_2 must therefore satisfy the following constraint:

$$(12)\quad \begin{aligned} &2\cdot(d_2 - d_1)/V < T - (2\cdot d_1/V + tF_1 + tH_1) \\ &d_2 < V/2\cdot\{T - [1 + h_A\cdot q_A\cdot D_A(d_1) + h_B\cdot q_B\cdot D_B(d_1)]\cdot tF_1\}. \end{aligned}$$

Provided the second site is feasible, the time available for fishing there is given by

$$(13)\quad \begin{aligned} &tF_2 = T - tS - tF_1 - tH_1 - tH_2 \\ &tF_2 = \\ &\frac{T - 2\cdot\max(d_1,d_2)/V - [1 + h_A\cdot C_A(d_1,tF_1) + h_B\cdot C_B(d_1,tF_1)]}{1 + h_A\cdot q_A\cdot D_A(d_2) + h_B\cdot q_B\cdot D_B(d_2)}. \end{aligned}$$

The time available for fishing at the second site is a function of d_1, tF_1, and d_2.

The skipper's revenue and cost flows can also be written as functions of d_1, tF_1, and d_2. If there are no binding trip limits, then the revenue function is

$$(14a)\quad R(d) = S\cdot\{p_A\cdot[C_A(d_1,tF_1) + C_A(d_2,tF_2)] + p_B\cdot[C_B(d_1,tF_1) + C_B(d_2,tF_2)]\}.$$

If the trip limit is binding on species A, for example, then the revenue function is

$$(14b)\quad R(d) = S\cdot\{p_A\cdot\text{limit}_A + p_B\cdot[C_B(d_1,tF_1) + C_B(d_2,tF_2)]\}.$$

The cost function is

$$(15)\quad K = pE\cdot[uS\cdot 2\cdot\max(d_1,d_2)/V + uF\cdot(tF_1 + tF_2)] + W\cdot T + kM.$$

Given the skipper's choice for d_1 and tF_1, and given values for the fish prices p_A and p_B, and all the other parameters of the model, it is possible to determine $d_2^*(d_1,tF_1)$, the fishing location that produces the largest profit flow per trip (for the given values of d_1 and tF_1). As in the earlier model, discontinuities arise in the revenue function when there is a binding trip limit. I used numerical techniques to solve for $d_2^*(d_1,tF_1)$ for particular sets of parameter values (Table 2).

Results for the Extended Model

Figure 4 depicts a situation in which the two stocks are well separated and there is a relatively large but binding

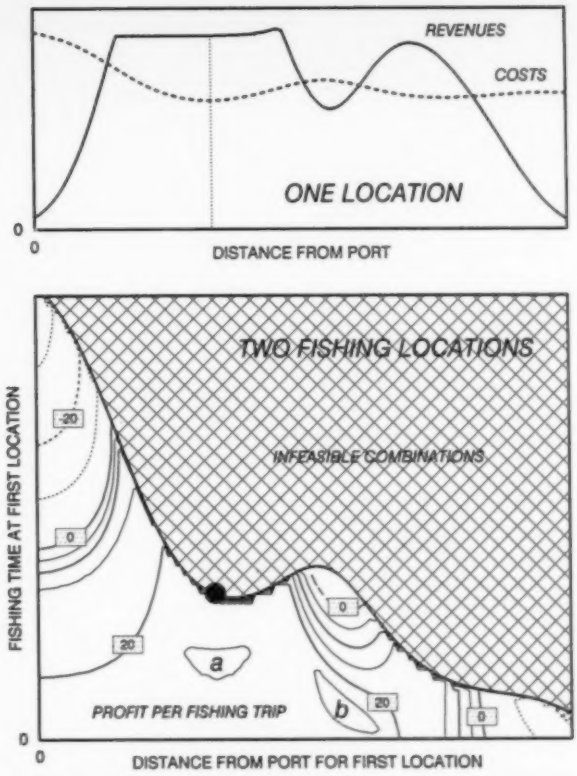


FIG. 4. When trip limits on species A are binding, the optimum fishing strategy can be to fish at more than one location. In this example, the profits per trip from fishing at the single best location (top panel, vertical dotted line) are about 15% smaller that the profits from fishing at the best combination of two fishing locations (bottom panel, regions *a* and *b*). The shaded region shows combinations of fishing and steaming time (location) that exceed the fixed duration of the trip.

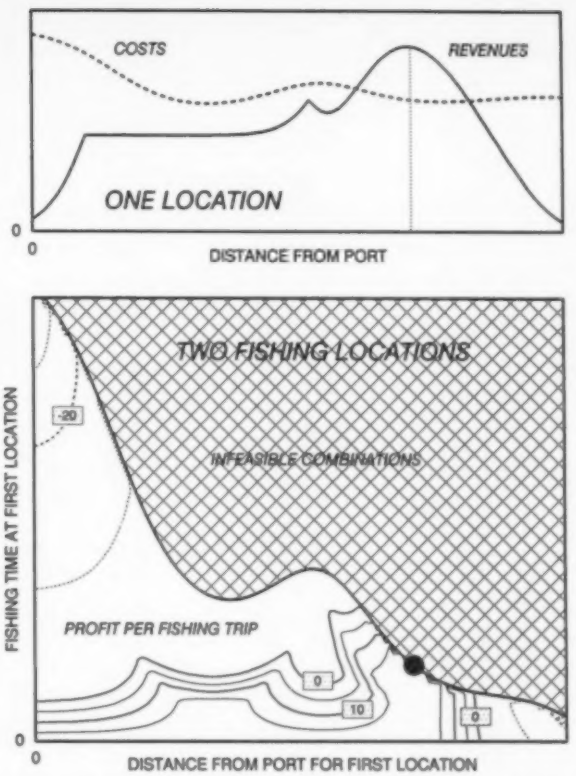


FIG. 5. The optimum fishing strategy can be to fish at a single location. In this example, the trip limit on species A is half the limit that applied in Fig. 4. In the bottom panel the combinations of fishing time and location that produce the maximum profit flow occur either at the boundary of the region of infeasible combinations, in which case the fishing time at the second site is zero, or along the horizontal axis, in which case the fishing time at the first site is zero.

trip limit on the landings of species A. The top panel shows how revenues and costs vary with fishing location if the skipper operates at a single location; the vertical dotted line represents the location that produces the maximum profit flow. The bottom panel shows how profit flow varies with different combinations of location (d_1) and fishing time (tF_1) if the skipper fishes at two locations, d_1 and $d_2^*(d_1,tF_1)$. The shaded region represents infeasible combinations of d_1 and tF_1. To operate using these values would require more time for the fishing trip than is available. Values at the boundary of the region of infeasible combinations represent trips in which fishing occurs at only one location and $tF_2 = 0$. The boundary values are given by eq. 7.

There are two regions in Fig. 4, labeled *a* and *b*, that produce the maximum profit flow; the profits from operating using these combinations of d_1 and tF_1 are significantly higher than the profits from operating at the optimum single location (marked in the figure by the solid circle). In this example, the best strategy is to fish where species A is most dense for just long enough to catch the trip limit and then move offshore to catch species B. Of course, it does not matter whether the fisher first catches the limit of species A and then catches species B, or vice versa; hence, there are two regions in the figure that correspond to maximum profitability.

Figure 5 shows a situation that is identical to the one on which Fig. 4 is based except that there is a smaller trip limit on species A. In this case the best fishing strategy is to fish at a single location, indicated in the top panel by the vertical dotted line and marked in the bottom panel by the solid circle. The highest profits occur either if tF_1 is zero (along the horizontal axis) or if tF_2 is zero (along the boundary of the region of infeasible combinations of d_1 and tF_1).

Discussion

In this paper the model for fishing location choice assumes that the duration of a fishing trip is a fixed and binding constraint that is known by the skipper at the outset of the trip. For some fisheries, this assumption is unrealistic and the model in this paper is inappropriate. For example, larger fishing boats that process and freeze their catches at sea can remain away from port for extended periods because they suffer less from deteriorating fish quality with increasing trip length. One can relax the assumption of a fixed trip length, but one must impose some form of constraint on

the fisher's activities or the fisher would never return to port. In Sampson (1991), I developed a model for a fishing trip in which the boat remains at sea until the fish hold is full. In this case the skipper's revenue per trip is fixed and only the operating costs vary with the choice of fishing location. This alternative constraint would also apply if there were binding trip limits on all available species; the boat would return to port as soon as it caught the trip limits.

One aspect of a fisher's decision making that I have not considered in this paper is whether or not the skipper would make a fishing trip at all. If fish prices or fish biomass are too low, then the skipper's profit-maximizing activity might be to remain in port rather than incur a loss (Sampson 1991, 1992). To model this decision, one must consider the opportunity cost of the skipper's labor. The skipper may find it more satisfying to remain ashore rather than making a fishing trip that earns a pittance. However, in modeling the decision of where to fish, as opposed to whether to fish, the opportunity costs of labor and capital are irrelevant.

Other aspects of the model that merit further attention are the assumptions that skippers know the spatial distributions of the fish and that they operate their boats to maximize profit flow. In general the catch rates at any given location are highly variable. It seems likely that fishers would consider the relative variability when choosing between two locations that yield the same average catch rate. However, it is unclear whether they would prefer the location with the more variable catch rates or the one with the less variable catch rates. Dupont (1993) found that some fishers were risk-prone and favored variability, while others were risk-neutral or even risk-averse.

Although the model in this paper is reasonably simple (perhaps unrealistically so), it can produce remarkably complicated behavior, such as switching between species (Fig. 1) and the strategy of fishing at two locations (Fig. 4). I suspect that other complexities are hidden in the mathematics. It would be particularly useful to examine more thoroughly the conditions that produce bycatch and discarding.

Simulations with the model over a wide range of parameter values suggest that the following proposition is valid. Given that a fisher seeks to maximize profits and has perfect knowledge of fish distributions, prices, and costs, a fisher will never fish at more than one location during a trip unless there are binding trip limits. Without binding limits, either regulatory or market ones, the best strategy is to fish at a single location, for to move from that best location results in lower catch rates and smaller profit flows. It would be instructive to evaluate this notion by examining detailed logbook information from some fisheries.

Preliminary results also indicate that trip limits can be effective at altering the fishers' behavior, but only if the fish stocks are reasonably well separated. If species that are regulated using trip limits co-occur with unregulated ones, then fishers cannot avoid catching the regulated species unless they forgo fishing altogether. A trip limit in this case results in incidental bycatch and discard of the regulated species. This last result is consistent with the findings of Squires and Kirkley (1991). In their econometric study of the trawl fishery off Eureka, California, they found that fishers had limited ability to reorganize their operations in response to a trip limit on sablefish, with the result that the excess production of sablefish was discarded at sea.

Acknowledgments

This work was partially supported by grant No. NA89AA-D-SG108 (project No. R/ES-16) from the National Oceanic and Atmospheric Administration (NOAA) to the Oregon State University Sea Grant College Program and by appropriations made by the Oregon State Legislature. The views expressed herein are those of the author and do not necessarily reflect the views of NOAA or any of its subagencies. Additional support for this work was provided by the Oregon Department of Fish and Wildlife and the Agricultural Experiment Station of Oregon State University.

References

ALLEN, P.M., AND J.M. MCGLADE. 1986. Dynamics of discovery and exploitation: the case of the Scotian shelf groundfish fisheries. Can. J. Fish. Aquat. Sci. 43: 1187–1200.

ANDERSON, L.G. 1986. The economics of fisheries management. Revised and enlarged edition. Johns Hopkins University Press, Baltimore, Md. 296 p.

ANTHONY, V.C. 1990. The New England groundfish fishery after 10 years under the Magnuson Fishery Conservation and Management Act. N. Am. J. Fish. Manage. 10: 175–184.

CAMPBELL, H.F. 1991. Estimating the elasticity of substitution between restricted and unrestricted inputs in a regulated fishery: a probit approach. J. Environ. Econ. Manage. 20: 262–274.

DUPONT, D.P. 1993. Price uncertainty, expectations formation and fishers' location choices. Mar. Res. Econ. 8: 219–247.

EALES, J., AND J.E. WILEN. 1986. An examination of fishing location choice in the pink shrimp fishery. Mar. Res. Econ. 2: 331–351.

FRETWELL, S.D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, N.J. 217 p.

GILLIS, D.M., R.M. PETERMAN, AND A.V. TYLER. 1993. Movement dynamics in a fishery: application of the ideal free distribution to spatial allocation of effort. Can. J. Fish. Aquat. Sci. 50: 323–333.

GULLAND, J.A. 1955. Estimation of growth and mortality in commercial fish populations. U.K. Minist. Agric. Food Fish. Fish. Invest. Ser. 2, 18(9): 46 p.

HEALEY, M.C., AND J.F.T. MORRIS. 1992. The relationship between the dispersion of salmon fishing vessels and their catch. Fish. Res. 15: 135–145.

HILBORN, R., AND M. LEDBETTER. 1979. Analysis of the British Columbia salmon purse-seine fleet: dynamics of movement. J. Fish. Res. Board Can. 36: 384–391.

HILBORN, R., AND C.J. WALTERS. 1987. A general model for simulation of stock and fleet dynamics in spatially heterogeneous fisheries. Can. J. Fish. Aquat. Sci. 44: 1366–1369.

MANGEL, M., AND C.W. CLARK 1983. Uncertainty, search, and information in fisheries. J. Cons. int. Explor. Mer 41: 93–103.

PACIFIC FISHERY MANAGEMENT COUNCIL. 1993. Pacific coast groundfish management plan: fishery management plan for the California, Oregon and Washington groundfish fishery as amended through Amendment 7. Pacific Fishery Management Council, 2000 SW First Avenue, Suite 420, Portland, OR 97201.

PIKITCH, E.K., D.L. ERICKSON, AND J.R. WALLACE. 1988. An evaluation of the effectiveness of trip limits as a management tool. National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Processed Rep. 88-27: 33p.

SAMPSON, D.B. 1991. Fishing tactics and fish abundance, and their influence on catch rates. ICES J. Mar. Sci. 48: 291–301.

SAMPSON, D.B. 1992. Fishing technology and fleet dynamics: predictions from a bioeconomic model. Mar. Res. Econ. 7: 37–58.

SQUIRES, D., AND J. KIRKLEY. 1991. Production quota in multiproduct Pacific fisheries. J. Environ. Econ. Manage. 21: 109–126.

SUTINEN, J.G. 1979. Fishermen's remuneration systems and implications for fisheries development. Scott. J. Polit. Econ. 26: 147–162.

TYLER, A.V. 1988. Biological basis for management of groundfish resources of the west coast of Canada. p. 217–232. *In* W.S.Wooster [ed.] Fishery science and management: objectives and limitations. Springer-Verlag, New York, N.Y. 339 p.

Sensitivity of Optimum Harvest Strategy Estimates to Alternative Definitions of Risk

Bernard A. Megrey and Anne Babcock Hollowed

U.S. Department of Commerce, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA, 98115, USA

and Rebecca T. Baldwin

U.S. Department of Agriculture, U.S. Forest Service, Alaska Regional Office, Federal Office Building, P.O. Box 21628, Juneau, AK, 99802, USA

Megrey, B.A., A.B. Hollowed, and R.T. Baldwin. 1994. Sensitivity of optimum harvest strategy estimates to alternative definitions of risk. Can. J. Fish. Aquat. Sci. 51: 2695–2704.

A stochastic age-structured bioeconomic simulation model was developed as a tool for evaluating economic returns to a fishery from alternative harvest policies. The model, which was applied to the Gulf of Alaska walleye pollock (*Theragra chalcogramma*) fishery, combines the dual goals of protection of the base stock and efficient use of the public resource into an explicit objective function. This paper presents the results of several experiments in which the simulation model is used to examine the sensitivity of the optimum harvest strategy estimates to alternative definitions of risk and assumptions regarding recruitment. Alternative definitions of risk consider assumptions about stock productivity, threshold biomass, economic factors, and hybrid formulations. The bioeconomic extension of the population dynamics model is used to quantify differences in the estimates of optimum fishing mortality obtained from the different risk definitions. Model results demonstrate that estimates of optimal fishing mortality and economic return to the fishery are sensitive to the specific definition of risk used to manage the fishery. The recruitment assumption turned out to be more important to optimum harvest strategy estimates than did risk definitions.

Un modèle de simulation bioéconomique stochastique structuré selon l'âge a été mis au point comme outil pour évaluer le rendement économique, pour la pêcherie, de différentes politiques de récolte. Le modèle, qui a été appliqué à la pêcherie de morue du Pacifique occidental (*Theragra chalcogramma*) du golfe d'Alaska, contient une fonction qui traite explicitement du double objectif que sont la protection du stock de base et l'utilisation efficace des ressources publiques. Le présent article présente les résultats de plusieurs expériences dans lesquelles le modèle a été utilisé pour examiner la sensibilité de valeurs estimées de la stratégie de récolte optimale à l'égard de plusieurs définitions différentes du risque et de plusieurs hypothèses concernant le recrutement. Les différentes définitions du risque tiennent compte d'hypothèses concernant la productivité du stock, la biomasse seuil, les facteurs économiques et des formulations hybrides. Le prolongement bioéconomique du modèle relatif à la dynamique des populations sert à quantifier les différences observées dans les valeurs estimées de la mortalité optimale par pêche obtenues à partir des différentes définitions du risque. Les résultats obtenus avec le modèle montrent que les valeurs estimées de la mortalité optimale par pêche et la rentabilité économique pour la pêcherie sont sensibles à la définition particulière du risque utilisée pour gérer la pêcherie. L'hypotèse sur le recrutement s'est révélée plus importante que les définitions du risque pour l'établissement des valeurs estimées de la stratégie de récolte optimale.

Received March 8, 1994
Accepted November 2, 1994
(J12309)

Reçu le 8 mars 1994
Accepté le 2 novembre 1994

Fishery managers operate in an environment of uncertainty. Excessively high harvest levels increase the likelihood of a stock collapse, while unnecessarily low levels reduce the economic return to the commercial fisheries and society. At the extreme, an $F = 0$ policy would not put an exploited stock at risk no matter how much uncertainty there was about stock status. Risk arises from imperfect knowledge of population life history parameters, unknown future recruitment, lack of precision in survey abundance estimates, the timeliness of data, little knowledge of the future value of the stock, and the relative value of the investment of resources in the fishery. Recently the topics of risk evaluation, methodologies for quantifying and expressing uncertainty associated with biological reference points, and the communication of uncertainty to fisheries managers have received considerable attention (Shepherd 1991; Fogarty et al. 1992; Francis 1991, 1992; Hilborn et al. 1993; Smith 1993; Smith et al. 1993; Cordue and Francis 1994).

The recent attention devoted to the application of risk evaluation to fisheries management is mainly due to advances in stock assessment methods and the ability to quantify uncertainties in key parameters. However, the communication of risk to fisheries managers by scientists is hindered by a lack of well-defined objectives for fisheries management (Smith 1993) as well as clear guidelines for the identification and definition of risk. There are many ways to define risk.

Some definitions include only biological considerations such as stock issues (i.e., MSY) or fisheries issues (i.e., limits on TAC's). Some definitions only deal with economic considerations (i.e., maximizing net economic return), while others blend both biological and economic aspects. Furthermore, any of these definitions of risk can be combined into hybrid formulations. The problem faced by fisheries scientists and often fisheries managers is that, of all the possible candidate definitions, they do not know which objective functions to optimize.

The objective of this study is to propose a bioeconomic modelling framework for the evaluation of risk and the identification of an optimal fishing policy, and then to examine the sensitivity of the optimal solution to the alternative definitions of risk. The utility of the model in evaluating questions of risk was demonstrated through an application to the Gulf of Alaska walleye pollock (*Theragra chalcogramma*) fishery.

Background

Walleye pollock in the Gulf of Alaska are harvested almost entirely by midwater trawl. The fishery is made up of a harvesting and a processing component. The catch is taken by a fleet of trawl catcher boats that deliver their catch to shoreside processing plants. A portion of the catch is also taken by a number of floating processors which harvest and process pollock while at sea. Because of current management allocation policies, the bulk of the pollock catch is delivered to shoreside plants for processing. Typically, fish ages 3 to 10+ appear in the catch.

Pollock are processed into three primary products: roe, surimi, and fillets. Roe, a relatively high-valued product compared with either surimi or fillets, is taken early in the year during the pollock spawning season. Pollock flesh is processed into either surimi (a paste made of fish flesh) or fillets. The decision of an at-sea or shoreside processing plant to produce either surimi or fillets is a function of the plant structure, size of the fish, and market conditions. However, for the industry as a whole, during the last half of the year, older fish are turned into fillets instead of surimi because in recent years, fillets have commanded a premium price. Thus, harvest strategies which result in more older and thus larger fish being caught will result in more fillets being produced and a corresponding higher economic value to the fishery. We assume that the relative real prices of the three products remain fixed and exogenous to the model. This is a reasonable assumption because the amount of pollock that could be harvested in the Gulf of Alaska is small in comparison with pollock harvests in other areas of the North Pacific. The number of active fisheries limits the ability for changes in production levels from the Gulf of Alaska fishery to influence prices. In addition, fillets of other species such as Pacific whiting (*Merluccius productus*) or Pacific cod (*Gadus macrocephalus*) can be substituted for pollock in the marketplace during the production of surimi or fillets.

The Gulf of Alaska walleye pollock fishery is a good candidate for application of the modelling technique described in the next section because pollock exhibit wide interannual variations in recruitment (Hollowed et al. 1991; Schumacher and Kendall 1991) and survey and fishery data contain inconsistencies which may contribute to errors in the stock assessment (Megrey et al. 1990). In addition, the current configuration of the commercial operation in the Gulf of Alaska allows us to use a relatively simple structure in the economic model to capture the variable return to this sector.

Methods

A stochastic age-structured bioeconomic simulation model was developed as a tool for evaluating optimal harvest policies and for calculating economic returns to a fishery. The model presented here is the third generation of simulation models developed for analysis of harvest policies for the walleye pollock fishery. The original version, a stochastic age-structured Monte Carlo simulation model, was developed to examine constant catch fishing policies (Megrey 1989). Hollowed and Megrey (1993) modified this model to explore constant fishing mortality policies and extended it to incorporate explicit calculations of risk. This was then later adapted to accommodate bioeconomic features after Baldwin and Megrey (1990). The current model configuration combines the dual goals of protection of the base stock during low stock levels and efficient use of the public resource into an explicit objective function.

The main features of the model include (1) an explicit description of process error in the estimation of recruitment and measurement error in the stock assessment procedures, (2) a bioeconomic submodel to translate yield in biomass into monetary units discounted to present value, (3) a formal objective function designed to identify the level of optimal fishing mortality, (4) simultaneous tracking of two realizations of the population similar to the approach taken by Shelton et al. (1993) and Pelletier and Gros (1991): a true population and a perceived population, and (5) use of Monte Carlo simulation to assess risk. The objective function combines the goals of optimizing yield at high stock levels and protecting the stock during periods of low abundance. Bioeconomic features of the model are used to compute the foregone value arising from having to manage conservatively.

The biological model is age structured and follows the operation of the fishery over two periods of the year: winter–spring and summer–fall. Selectivity vectors for the simulations were based on selectivity patterns estimated from fisheries data. We provide a description of the major features of the model reported in Hollowed and Megrey (1993) for background purposes so that the reader can fully understand the model structure, the nature of the stochastic processes, and simulation mechanics.

An important feature of the biological model is a stochastic recruitment generator and the ability to track both process error associated with recruitment variability and measurement error in stock assessments. Process error in recruitment variability was modelled using a nonparametric classification scheme based on planes of the stock–recruitment graph (Rothschild and Mullen 1985). Other authors have generated recruitment estimates using probability density functions of recruitment at a given stock size (Getz and Swartzman 1981; Brown and Patil 1986; Linder et al. 1987; Evans and Rice 1988). A nonparametric scheme for describing recruitment was chosen because of the high variability in the information describing the stock abundance and recruitment data. Data were so variable as to preclude fitting a useful parametric function.

Estimates of spawner stock biomass and recruitment were obtained from the stock assessment (Hollowed et al. 1991). We divided the stock–recruit graph into four quadrants by the

TABLE 1. Parameter values used in the stochastic recruitment generator and the measurement error components of the biological simulation model.

Recruitment assumption	Recruitment state probability	Recruitment values (billions)	Number of observations
High	Pr(high recruitment | low spawning biomass) = 0.70	$R \sim N(1.940,0.954)$	7
High	Pr(high recruitment | high spawning biomass) = 0.36	$R \sim N(0.904,0.317)$	4
High	Pr(low recruitment | low spawning biomass) = 0.30	$R \sim N(0.213,0.057)$	3
High	Pr(low recruitment | high spawning biomass) = 0.64	$R \sim N(0.277,0.147)$	7
Low	Pr(high recruitment | low or high spawning biomass) = 0.40	$R \sim N(0.904,0.317)$	4
Low	Pr(low recruitment | low or high spawning biomass) = 0.60	$R \sim N(0.255,0.147)$	6

Recruitment measurement probabilities
(probability of accurately estimating the magnitude of the incoming year class)

Age	3	4	5	6	7	8	9	10
Probability	0.30	0.26	0.22	0.18	0.14	0.10	0.06	0.02

median recruitment (1.7 billion) and median spawner biomass (0.998 million t). Selection of the median value as the cutoff values followed Rothschild and Mullen (1985); however, other cutoff values could have been determined. The number of data points in each quadrant describes the empirical probability of a high (HR) or low (LR) recruitment condition given a spawning biomass condition. The conditional probability of HR or LR was estimated by dividing the number of HR or LR observations by the total number of points observed at high or low spawner biomass levels.

Recruitment values were generated in two steps. First, a Bernoulli trial with probability dependent on current stock biomass determined whether recruitment was high or low. Second, a random recruitment value was selected from a normal distribution with mean equal to observed average recruitment of the appropriate quadrant and variance arbitrarily scaled so that the range of recruitment observations within the cell spanned three standard deviations.

At low levels of spawner abundance the probability of strong recruitment was parameterized so that two conditions occur as spawning biomass approaches zero: the probability of falling in the high recruitment plane approaches zero and the mean recruitment level approaches zero. The threshold spawning biomass was also set at 20% of the unfished spawner biomass. Details on this parameterization can be found in Hollowed and Megrey (1993).

Measurement error is related to our inability to accurately estimate the magnitude of incoming year classes until they have been monitored for several years through commercial fishery and survey catch-at-age information. This uncertainty in recruitment was addressed by modelling two populations: "true" and "perceived." Similar strategies have been adopted in simulation models for capelin (*Mallotus villosus*), Atka mackerel (*Pleurogrammus monopterygius*), and Atlantic cod (*Gadus morhua*) (Pelletier and Laurec 1992; Shelton et al. 1993; Lowe and Thompson 1993). As a cohort of fish moves through the population, they are observed in the catch during sequential fishing seasons at different ages. As the fish age, estimates of the cohort that produced the year class become more accurate. Thus the precision of year-class strength estimates is a function of age. The true population was computed from the recruitment generator, annual survival, and catch. Recruitment to the perceived population was set to the true population recruitment but adjusted by a uniformly distributed random measurement error term in the following manner. If η is the age-specific measurement error, ρ is a uniformly distributed random variable between 0 and 1, and RT is the true population recruitment value calculated from the nonparametric procedure described above, then recruitment to the perceived population (RP) was calculated as

$$\begin{aligned} RP &= RT\cdot(1 + [(\eta\cdot(1 - \rho)) - (\eta\cdot\rho)]) \\ &= RT\cdot(1 + \eta - \eta\cdot\rho - \eta\cdot\rho) \\ &= RT\cdot(1 + \eta\cdot[1 - 2\cdot\rho]). \end{aligned}$$

Parameter values for the recruitment generator and the measurement error stochastic process are given in Table 1.

TABLE 2. Economic parameters used in the model.

Ex-vessel price	US$249/t
Harvesting cost	US$44/t
Boat share	64%
Yield of surimi	0.194
Market price for surimi	US$3,131/t
Yield of fillets	0.184
Market price for fillets	US$3,571/t
Length of roe season	3 mo
Yield of roe	0.03
Market price for roe	US$11,417/t
Processing cost	US$595/t
Discount rate	4%/yr

NOTE: These parameters reflect estimates used in the North Pacific Fishery Management Council's Inshore/Offshore Amendment 18/23, updated to 1992.

The economic submodel measures the stream of annual gross revenues from all products minus the variable operating costs for both the catcher fleet and the shoreside processor sectors as the return to the fishery. Because the model runs provide annual projections of harvest and biomass for 50 yr into the future, a listing of the outputs solely in terms of physical units would not provide policy makers with a useful method for assessing trade-offs. Are we better off with higher harvests in the near future, even if that drastically increases the reduction of harvest in later years? Differences in the optimum management strategy are quantified as the stream of revenue measured as present discounted value using the results from an economic submodel. By discounting, we are able to make uniform comparisons of

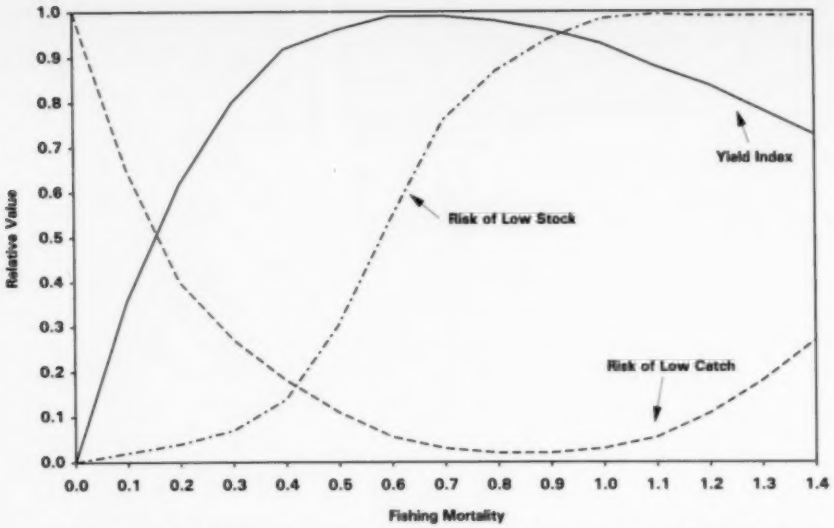


FIG. 1. Generalized relationship illustrating the relationship between two different possible definitions of risk and an index of yield.

the value received at different points in time. A complete description on the economic submodel is provided in the Appendix and the economic parameters are given in Table 2.

While vessels and plants can be involved in other fisheries that provide revenue beyond the receipts in the pollock fishery, we are only focusing on the returns from the pollock fishery. Thus, the present discounted values reported here do not reflect overall profit to the two sectors. For the same reason, fixed costs of the vessels and plants are not included in the economic submodel, as these would have to be distributed across all the different fisheries and products produced. The economic submodel focuses only on the variable costs incurred in this pollock fishery and does not capture entry of individual operators caused by changes in relative value between this and other fishery opportunities.

The following are several operating assumptions incorporated into the economic submodel. Observed changes in the value of the fishery are driven primarily by the modelled physical changes in the stock. We ignore multispecies concerns or bycatch issues because the catch in the Gulf of Alaska is almost purely pollock. Because current management imposes a ban on roe-stripping (removing the roe and discarding the carcass), we assume that during the first season, in addition to roe production, the flesh from all pollock age groups is converted into surimi. Because the flesh of older aged pollock is soft during this time of year, it is less desirable for fillet production.

The simulation model was run over a 70-yr time horizon. Observed age composition and abundance data from the beginning of the fisheries statistics time series (1976) were used to initialize the model. Observed catches from 1976 to 1989 were removed from the simulated population. For the remaining years in the simulation, fishery removals and simulated population dynamics were determined based on the specific harvest strategy, recruitment scenario, and risk definition being investigated. One hundred realizations of each 70-yr stochastic simulation experiment were computed. In order to minimize the effects of transient model behavior associated with imposed initial conditions, summaries of the long-term productive potential of the pollock stock were based on the results of the last 50 yr of the 70-yr projection. Variability of abundance and yield were expressed by coefficients of variation (CV's).

For each definition of risk, the simulation model was run under an above-average and below-average recruitment assumption. Hereafter we refer to these as the high and low recruitment assumption, respectively. Estimates of recruitment patterns for walleye pollock (Hollowed and Megrey 1993) indicate that recruitment has been at a relatively low to moderate level since 1962, punctuated by a series of five strong back-to-back year classes between 1975 and 1979. Over the recent 10-yr time period, there have been few strong year classes. Estimates of average recruitment at lower biomass levels are very sensitive to the inclusion of strong year classes. Using two recruitment assumptions facilitates the ability to ascertain the sensitivity of the optimum fishing mortality estimates to abrupt changes in recruitment such as those encountered in response to climate change. The high recruitment assumption uses averages and probabilities calculated from the entire recruitment time series, while the low recruitment assumption uses data points from the last 10 yr (1980–89) to calculate these quantities. Values of the stochastic recruitment generator parameters for both assumptions are given in Table 1.

There are many potential definitions of optimal fishing mortality. We examined the trade-offs between increased yield and the various definitions of risk. Risk in our analysis is defined as the probability of achieving a predefined goal such as maintaining a spawning biomass above some threshold value. Risk can also be classified relative to the type of goal fisheries management is attempting to satisfy. For example, risk can represent a probability of a failed attempt to attain something such as a predetermined precision in TAC, a sufficient level of harvest to maintain the financial investment in the fishery at its current level, or a failed attempt to avoid something such as a spawning biomass target or threshold. As fishing mortality increases, we expect yield or yield relative to some benchmark like MSY (yield

index) to increase to a point of diminishing return (Fig. 1). Risk is also a function of fishing mortality, but the shape of the risk curve depends on the risk definition. Figure 1 describes two risk definitions. Risk of low stock will be low at a low levels of F and increase with F until the probability reaches a value of 1.0. Risk of low catch will be high for low values of F and decreases with increasing F to some minimum and then increases with increasing F. Optimal fishing mortality is defined as the maximum difference between the yield index curve and the risk curve; in other words, the fishing mortality that gives us the maximum yield with minimum risk.

We explored three definitions of risk. The first addressed a biological aspect of the stock. We defined risk as the probability of the spawning biomass falling below a threshold. This is a common definition of risk that is based on convincing biological arguments. The threshold defines the population level below which there is a concern over the ability of the stock to rebuild over an acceptable planning horizon. A threshold set too low will not provide adequate protection to the stock and may prevent the stock from rebuilding whereas a threshold set too high deprives harvesters of fishing opportunities. In response to these competing goals, an objective function to examine optimal fishing mortality using the threshold biomass definition of risk was formulated as

$$(1)\quad \mathrm{MAX}[(Y_F/\mathrm{Max}Y) - \{\Pr(\mathrm{SB} < \alpha)|F\}]$$

where average Y_F equals the yield over the 50-yr time period at a given level of F, Max$Y$ is the maximum average yield observed over all levels of F, Pr is the probability of the spawning biomass falling below the threshold given the level of F, SB is the spawning biomass, and α is the threshold biomass. In our model, the threshold biomass was set to 20% of the virgin spawning biomass or 380 000 t (Hollowed and Megrey 1993). The values used in the objective function were averaged over 100 Monte Carlo realizations of the stochastic simulation. Risk probability was calculated as the average of 100 probabilities, each of which was calculated as the number of years out of the last 50 in the simulation that the spawning biomass fell below the threshold. The optimal value of F was determined by iteratively solving for the fishing mortality value that maximized the objective function. Also the 100 stochastic recruitment trajectories were different for all F levels. For example, the third recruitment trajectory for $F = 0.1$ was different from the third trajectory for $F = 0.2$

The second definition of risk attempts to address the risk to the fishery of not having a high enough return to maintain the industry at its current level. As individual operators see a decline in their overall return from this stock, they may decide to leave the market, which can impose negative social costs on local communities and workers. We defined risk as the probability of the catch biomass falling below 75 000 t. This level of catch approximates the lowest level of catch observed during the period when the fishery was dominated by domestic fishing operations (Hollowed et al. 1991). The objective function used to examine optimal fishing mortality using the catch biomass definition of risk was

$$(2)\quad \mathrm{MAX}[(Y_F/\mathrm{Max}Y) - \{\Pr(\text{catch biomass} < \phi)|F\}]$$

where the variables are as defined in (1) and ϕ, which is the target catch biomass that preserves the industry status quo, is set to 75 000 t. With some minor modifications of the economic submodel, this concern about reduction of the industry could be captured with a definition of risk expressed solely in monetary units based on the probability of the economic return falling below the shutdown level. Shutdown of production would occur when price did not cover the average variable costs associated with production at any level of feasible output.

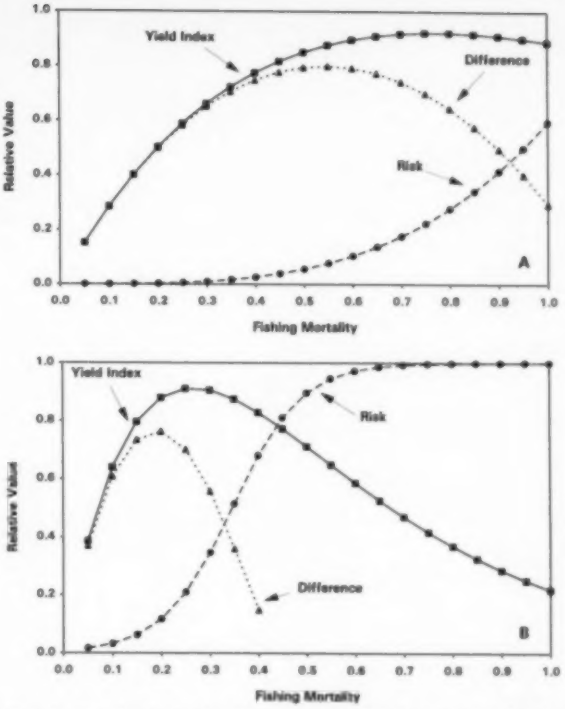


FIG. 2. Results from the bioeconomic simulation model using threshold biomass definition of risk. The yield index (solid line), risk (dashed line), and the difference (dotted line) are presented for (A) an above-average recruitment assumption and (B) a below-average recruitment assumption.

The third definition of risk follows Quinn et al. (1990). The goal of this definition is based on the premise that management of the fishery should provide protection for the population, result in a high yield, and avoid large annual variations in yield. The following compound objective function attempts to balance the trade-offs between increased yield and yield stability:

$$(3)\quad \mathrm{MAX}[(1 - \lambda)Y_F - \lambda \mathrm{SD}_{Y(F)}]$$

where Y_F is as defined in (1) and (2), $\mathrm{SD}_{Y(F)}$ is the standard deviation of yield given a fishing mortality F, and λ is a penalty weighting factor representing the cost of one unit of increase in standard deviation relative to one unit of increase in yield. The sensitivity of estimates of F to different values of λ was examined by changing the value of λ and recalculating the optimum F. A λ value of 0.5 was used in final model runs.

For each definition of risk, the simulation model was run under two different recruitment assumptions, above-average and below-average recruitment as defined above. Differences in estimates of optimum fishing mortality were quantified

TABLE 3. Estimates of yield, yield coefficient of variation (CV) optimum F, returns to the fishery accumulated over the 50-yr simulation horizon expressed as present discounted value (PDV), and expected risk under three definitions of risk and two recruitment assumptions.

Recruitment assumption	Risk definition	Objective function	Yield (1000 t)	Yield CV	Optimum F	PDV (billions)	Expected risk[a]		
							1	2	3
High	Threshold biomass	1	348.7	0.37	0.55	4.11	0.06	0.02	68.9
Low	Threshold biomass	1	67.5	0.38	0.17	0.80	0.10	0.65	12.8
High	Catch biomass	2	364.4	0.42	0.64	4.29	0.08	0.03	74.7
Low	Catch biomass	2	75.0	0.55	0.28	1.85	0.46	0.53	19.4
High	Yield stabillity	3 ($\lambda = 0.5$)	341.3	0.33	0.52	4.03	0.04	0.01	68.1
Low	Yield stability	3 ($\lambda = 0.5$)	74.8	0.52	0.21	0.90	0.20	0.53	15.6

[a]1, Risk calculated from objective function 1 Pr(SB < α); 2, risk calculated from objective function 2 Pr(catch biomass < ϕ); 3, risk calculated from objective function 3 $\lambda SD_{Y(F)}$.

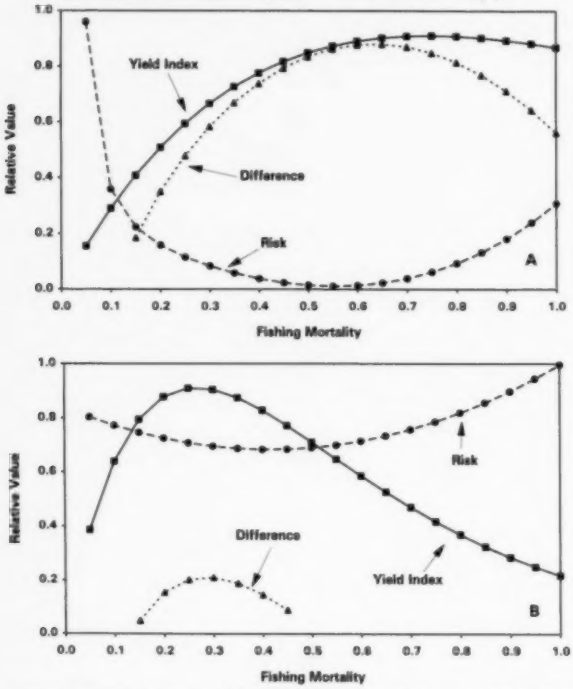


FIG. 3. Results from the bioeconomic simulation model using catch biomass definition of risk. The yield index (solid line), risk (dashed line), and the difference (dotted line) are presented for (A) an above-average recruitment assumption and (B) a below-average recruitment assumption.

by comparing the estimates of present discounted value (PDV) calculated from the economic submodel. Similar to Monte Carlo statistics, the PDV values were calculated over a 50-yr time horizon using a real discount rate of 4%. This discount rate is an accepted standard in natural resource situations where the planning time horizon is long (Department of Commerce 1994).

Results

In the experiment using the threshold biomass definition of risk and the high recruitment assumptions (Fig. 2A) the yield index curve only proceeds to pass a maximum value for fishing mortalities (F) in excess of 0.8. The risk curve, while progressively rising with increasing F, only reaches a value of 0.6 for an F of 1.0. When the productivity of the stock is decreased due to a low recruitment assumption (Fig. 2B), the yield index curve has a well-established maximum at a much lower fishing mortality. We also see a typical expression of the risk curve, that is, a sigmoid-shaped curve that begins with low risk at low F, rises quickly at intermediate values of F when yield begins to taper off, and then rises to an asymptotic value with increasing F and decreasing yield.

Using the catch biomass definition of risk, the yield index responses to the recruitment assumptions (Fig. 3) are similar to those of the threshold biomass risk definition; however, the risk curves are very different. For the high recruitment assumption (Fig. 3A), at low values of F, the yield remains low and the risk of not achieving the required catch biomass to maintain an economically viable fishery is high. As F increases, yield increases, and the risk curve tapers off, gradually going to zero at F values around 0.5. For the low recruitment assumption (Fig 3B) the risk curve has a similar shape. Because the productivity of the stock is reduced, the risk curve has higher values at similar values of F when compared with Fig. 3A. In both cases the difference curve has a concave shape. As in the case of the threshold biomass definition of risk, optimum values of F are lower for the low recruitment assumption (Table 3).

Results using the yield variation definition of risk (Fig. 4) are very similar to the threshold biomass definition of risk results except that the curve of the standard deviation of yield has a linear shape for the high recruitment assumption (Fig. 4A) and a dome-shaped appearance similar to the yield curve in the low recruitment assumption (Fig. 4B). Consequently the difference curve is also dome-shaped in both instances, with a well-defined maximum in the case of the low recruitment assumption.

Using the threshold biomass definition of risk (Fig. 2) the optimum F was estimated to be 0.55 and 0.17 for the high and low recruitment assumption, respectively. Yield differed by about a factor of 5 due to the recruitment assumption alone. Estimates of optimum F from the catch biomass definition of risk (Fig. 3) were 0.64 and 0.28 for the high and low recruitment assumptions, respectively. Yields from this run were also different by about a factor of 5. The results from using the yield stability objective function (Fig. 4)

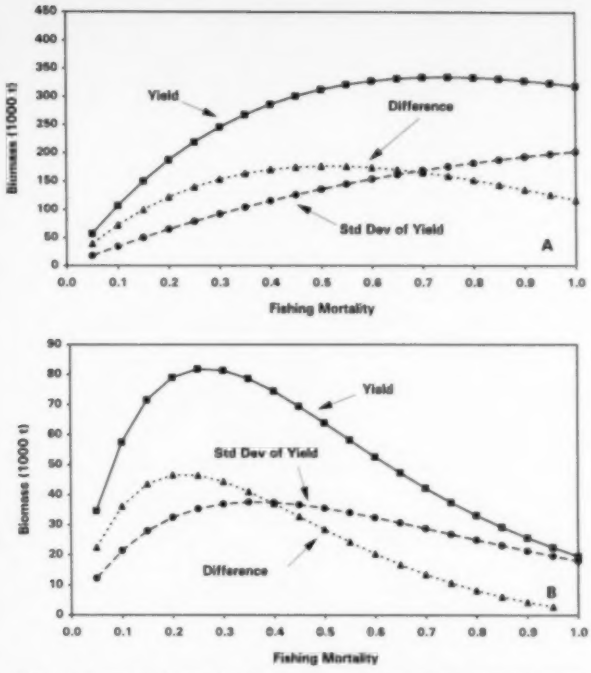


FIG. 4. Results from the bioeconomic simulation model using yield stability definition of risk. The yield index (solid line), risk (dashed line), and the difference (dotted line) are presented for (A) an above-average recruitment assumption and (B) a below-average recruitment assumption.

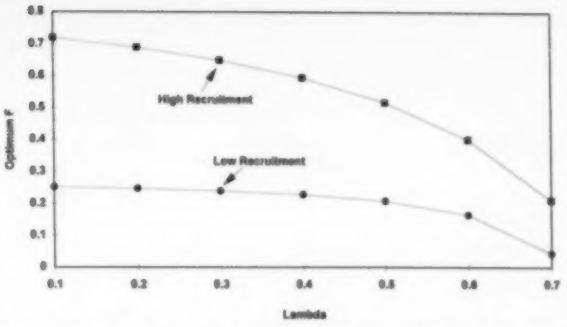


FIG. 5. Sensitivity of optimum fishing mortality estimates to values of the weighting factor (lambda) for two recruitment assumptions. Data are plotted using objective function 3.

were very similar to the threshold biomass definition of risk runs in the estimates of optimum F and yield.

A summary of simulation results is presented in Table 3. Each row in the table represents a simulation experiment using a given recruitment assumption and risk definition. Yield variability, expressed as a CV within a recruitment assumption was similar in the threshold biomass definition of risk, but about 30% different for the catch biomass definition, and 60% different for the yield variation definition. There was a tendency for yield variability to increase slightly with increased yield. Yield CV's were higher for the low recruitment assumption within the same risk definition.

Differences in estimates of economic returns to the fishery from the different methods of defining risk were similar for the high recruitment assumption but varied under the low recruitment assumption (Table 3). Using the high recruitment assumption, the net economic return to the fishery over the 50-yr simulation horizon expressed as present discounted value was $4.11 billion (U.S.) using the threshold biomass risk definition, $4.29 billion (U.S.) using the catch biomass risk definition, and $4.03 billion (U.S.) using the yield stability definition. The differences in the present discounted value between the different definitions of risk represent the cost of stability. Thus, in this example, if fisheries management used the yield stability definition of risk instead of the catch biomass or threshold biomass under the high recruitment assumption, the fishery would have lost the opportunity to realize an additional 2.0–6.5% increase in the present discounted value. Under the low recruitment assumption, this range was much higher and the rank order differed (i.e., yield stability was not the lowest in terms of present discounted value).

Expected risk estimates, presented for each simulation experiment in Table 3, allow direct comparisons of the trade-offs between the different policies. For example, even when fishing mortality is optimized for a catch biomass risk definition and the recruitment assumption is low, the catch biomass risk is 15% higher than the calculated threshold biomass risk.

Sensitivity of the estimates of optimum F to the weighting factor (λ) used in objective function 3 are given in Fig. 5 for the two recruitment assumptions. When λ is close to 0.0, the objective function weights the yield higher than the standard deviation of yield. The converse is true when λ is close to 1.0. In both recruitment cases, optimum F estimates are highest when λ is close to 0.0 and gradually decrease as λ goes to 1.0 (Fig. 5). In situations where yield variability is weighted more heavily than yield (λ near 1.0) the optimum F is low, while in situations where yield is weighted more heavily than yield variability (λ near 0.0) the optimum F is high. The change in F over the transition of λ going from 0.0 to 1.0 is a very gradual decrease, with the decrease sharply dropping after $\lambda = 0.6$. This pattern is similar for both recruitment assumptions although the slope of the decrease of F with increasing λ is a little greater for the high recruitment assumption. A relative change in λ from 0.5 to 0.4 (a 20% decrease) results in a 9.5 and a 15.1% increase in F for the low and high recruitment assumptions, respectively. A relative change in λ from 0.5 to 0.6 (a 20% increase) results in a 21.1 and a 22.4% decrease in F for the low and high recruitment assumptions, respectively. Thus the optimum estimate of F is slightly more sensitive to values of λ in the high recruitment assumption.

Discussion

Fisheries management is clearly a complex melding of biology, economics, sociology, and politics. Fisheries managers operate in an environment of uncertainty and imprecision. If managers do not take a conservative approach when information is absent, or there is concern about the precision of parameter estimates, they risk potential stock collapse. But this conservatism may come at the cost of lost fishing opportunities. Managers must constantly consider the trade-offs between lost short-term fishing opportunities and risk-adverse management because of uncertain information on stock

productivity. All interests stand to benefit if we can better understand the trade-offs made within the management arena. Towards this end, our bioeconomic simulation approach provides the capability of quantifying the cost of conservation, which is necessary for fisheries managers to make informed decisions regarding fishing policy (Clark 1980; Francis 1992; Pearse and Walters 1992).

The economic analysis has deliberately used many simplifying assumptions so that changes observed can be attributed to changes in the physical stock. This undoubtedly ignores many important considerations about this fishery. One of the most important may be the implicit assumption that the only source of economic value of this fishery is derived from its commercial use. For example, there is growing evidence that pollock may be an important source of food for Steller sea lions (*Eumetopias jubatus*) and other marine mammals (Pitcher 1991, 1980). Society derives benefits from the existence of these animals as well as utility from the consumption of the commercial pollock products. The existing model does not account for any increased risk to the other components of the ecosystem from the pollock removals. We may also have underrepresented the costs associated with low stock size because there is limited feedback in the model used in this study. In addition, while the concept of threshold spawning biomass is useful and has biological appeal, it is a rather vague concept. In our set of simulations, we assume that the threshold is an intrinsic biological characteristic of the stock and is not related to any particular recruitment assumption. Others might argue that the threshold biomass is a function of the ecosystem dynamics; thus, it is a quantity that changes from year to year or just simply from recruitment assumption to recruitment assumption (i.e., 20% of virgin spawning biomass will be different for different states of the system). Another strong assumption is that the economic setting described in the simulation model will be static over the 50-yr simulation horizon. Economic returns to the fishery and net revenues forgone to the industry, attributable to management actions, are critically contingent upon our economic assumptions being static over the 50-yr simulation horizon. These include assumptions regarding fixed product proportions, size composition of the stock, product form (pollock roe versus surimi versus fillets) and relative price, capital base, consumer tastes and preferences, and technology. Finally, we assume that omitting the at-sea processor sector does not materially affect our conclusions, as this economic component catches and processes only a small fraction of the overall harvest compared with in-shore processors. Because of the simplifying assumptions mentioned above, the reader should use caution in drawing conclusions from the bioeconomic model's output in an absolute monetary sense. The numbers presented rely heavily on a set of strong simplifying assumptions. However, the results are still useful for comparing risk strategies, as they permit uniform comparisons of the economic return to the fishery at different points in time.

We emphasize that the definitions of risk used in this paper are only a few of many possible definitions. Smith (1993) provided other possible definitions. In addition to the objective functions described earlier, numerous alternative formulations are possible. We only considered optimum harvest strategies for fixed fishing mortality. Variable F strategies could also be examined when the objective function is, say, to minimize interannual variability in yield. Finally, we note that different conclusions would be expected if we had assumed some linkage between spawner biomass and recruitment or used a different set of baseline bioeconomic assumptions, especially given the long time horizon used in the simulation model.

The simulation experiments described here demonstrate that estimates of optimum fishing mortality and corresponding economic returns to the fishery are sensitive to the specific definition of risk used to manage the fishery. This finding underscores the need for management or decision makers to communicate to fisheries scientists a set of well-defined objectives for fisheries management. By incorporating economic consideration into the analysis, we were able to provide a uniform quantitative measure for comparing trade-offs under different management policies. One implication of our exercise is that money spent on research, which should reduce the types of uncertainty described earlier, would lead to higher returns over time as management moved from a risk-averse position to a more risk-neutral stance. Powers and Restrepo (1993) addressed this problem by looking at the benefits of improved precision in combination with varying degrees of risk aversion.

One outcome of the simulation experiments is that the recruitment assumption is far more important to optimum harvesting strategy estimates than is the risk definition. A similar result was obtained by Hollowed and Megrey (1993). This result underscores the need to better understand the recruitment process and ecosystem response to climate change and ultimately to know the probability of a recruitment state. Research toward this end is underway in NOAA's Fisheries-Oceanography Coordinated Investigations Program. The primary goal of this multidisciplinary research program is to understand life stage interactions and environmental processes that lead to enhanced or reduced recruitment in walleye pollock. Recent research (Megrey et al. 1995) should improve the ability to predict year-class strength of this important commercial species.

We believe that use of bioeconomic fisheries models will improve the quality of fisheries policies by merging biological objectives with economic and social objectives. Our approach integrates and jointly considers biological and economic issues. The integrated approach is advantageous because often a stock can be reduced to a level of economic overfishing before the biological threshold is reached.

Asckowledgments

The authors would like to thank Drs. Richard Methot, Lewis Queirolo, David Somerton, and Vidar Wespestad for reading early drafts of the paper, as well Drs. Victor Restrepo and Pamela Mace for their thoughtful reviews. Numerous helpful discussions with Dr. Richard Methot improved and clarified our exposition. This research was conducted as part of NOAA's Fisheries-Oceanography Coordinated Investigation (FOCI) Program, Contribution No. FOCI-0210, U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, National Marine Fisheries Service, Seattle, Washington.

References

BALDWIN, R.T., AND B.A. MEGREY. 1990. Bioeconomic simulation model of the walleye pollock fishery in the Gulf of Alaska. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-145: 26 p.

BROWN, B., AND G.P. PATIL. 1986. Risk analysis in the Georges Bank haddock fishery — a pragmatic example of dealing with uncertainty. N. Am. J. Fish. Manage. 6: 183-191.

CLARK, C.W. 1980. Towards a predictive model for economic regulation of commercial fisheries. Can. J. Fish. Aquat. Sci. 37: 1111–1129.

CORDUE, P.L., AND R.I.C.C. FRANCIS. 1994. Accuracy and choice in risk estimation for fisheries assessment. Can. J. Fish. Aquat. Sci. 51: 817–829.

DEPARTMENT OF COMMERCE. 1994. National Oceanic and Atmospheric Administration, Natural Resource Damage Assessment; Notice of Proposed Rulemaking. July 7, 1994, Vol. 59, U.S. Federal Register 59: 106.

EVANS, G.T., AND J.C. RICE. 1988. Predicting recruitment from stock size without the mediation of a functional relation. J. Cons. int. Explor. Mer 44: 111–122.

FOGARTY, M.J., A.A. ROSENBERG, AND M.P. SISSENWINE. 1992. Fisheries risk assessment: sources of uncertainty. Environ. Sci. Technol. 26: 440–447.

FRANCIS, R.I.C.C. 1991. Risk analysis in fishery management. NAFO Sci. Coun. Studies, 16: 143–148.

FRANCIS, R.I.C.C. 1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. Can. J. Fish. Aquat. Sci. 49: 922–930.

GETZ, W.M., AND G.L. SWARTZMAN. 1981. A probability transition matrix model for yield estimation in fisheries with highly variable recruitment. Can. J. Fish. Aquat. Sci. 38: 847–855.

HILBORN, R., E.K. PIKITCH, AND R.C. FRANCIS. 1993. Current trends in including risk and uncertainty in stock assessment and harvest decisions. Can. J. Fish. Aquat. Sci. 50: 874–880.

HOLLOWED, A.B., AND B.A. MEGREY. 1993. Evaluation of risks associated with application of alternative harvest strategies for Gulf of Alaska walleye pollock, p. 291–320. *In* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II [ed.] Proceedings of the International Symposium of Management Strategies for Exploited Fish Populations. Alaska Sea Grant College Program Report No 93-02, University of Alaska Fairbanks, Fairbanks, Alaska.

HOLLOWED, A.B., B.A. MEGREY, P. MUNRO, AND B. KARP. 1991. Walleye pollock, p. 1-1 to 1-92. *In* Stock Assessment and Fishery Evaluation Report for the 1992 Gulf of Alaska Groundfish Fishery. North Pacific Fisheries Management Council, P.O. Box 103136, Anchorage, AK 99510.

LINDER, E., G.P. PATIL, AND D.S. VAUGHAN. 1987. Application of event tree risk analysis to fisheries management. Ecol. Model. 36: 15–28.

LOWE, S.A., AND G.G. THOMPSON. 1993. Exploitation strategies for the Atka mackerel resource of the Aleutian Islands, p. 203–232. *In* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II [ed.] Proceedings of the International Symposium of Management Strategies for Exploited Fish Populations. Alaska Sea Grant College Program Report No 93-02, University of Alaska Fairbanks, Fairbanks, Alaska.

MEGREY, B. A. 1989. Population dynamics of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. Ph.D. Dissertation, University of Washington, Seattle, Wash. 385 p.

MEGREY, B.A., S.J. BOGRAD, W.C. RUGEN, A.B. HOLLOWED, P.J. STABENO, S.A. MACKOIN, J.D. SCHUMACHER, AND W.J. INGRAHAM, JR. 1995. An exploratory analysis of associations between biotic and abiotic factors and year-class strength of Gulf of Alaska walleye pollock. (*Theragra chalcogramma*). *In* R.J. Beamish [ed.] Climate change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. 121. (In press)

MEGREY, B.A., A.B. HOLLOWED, AND R.D. METHOT. 1990. Integrated analysis of Gulf of Alaska walleye pollock catch-at-age and research survey data using two different stock assessment procedures. Int. North Pac. Fish. Comm. Bull. 50: 279–302.

PEARSE, P.H., AND C.J. WALTERS. 1992. Harvesting regulation under quota management systems for ocean fisheries. Decision making in the face of natural variability, weak information, risks and conflicting incentives. Mar. Policy (May) 167: 182.

PELLETIER, D., AND P. GROS. 1991. Assessing the impact of sampling error on model-based management advice: comparison of equilibrium yield per recruit variance estimators. Can. J. Fish. Aquat. Sci. 48: 2129–2139.

PELLETIER, D., AND A. LAUREC. 1992. Management under uncertainty: defining strategies for reducing overexploitation. Int. Counc. Explor. Sea J. Mar. Sci. 49: 389–401.

PITCHER, K.W. 1980. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. Fish. Bull. U.S. 78: 544–549.

PITCHER, K.W. 1991. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish. Bull. U.S. 79: 467–472.

POWERS, J.E., AND V.R. RESTREPO. 1993. Evaluation of stock assessment research for Gulf of Mexico king makerel: benefits and costs to management. N. Am. J. Fish. Manage. 13: 15–26.

QUINN, T.J. II, R. FAGEN, AND J. ZHENG. 1990. Threshold management policies for exploited populations. Can. J. Fish. Aquat. Sci. 47: 2016–2029.

ROTHSCHILD, B.J., AND A.J. MULLEN. 1985. The information content of stock-and-recruitment data and its non-parametric classification. J. Con. int. Explor. Mer 42: 116–124.

SCHUMACHER, J.D., AND A.W. KENDALL, JR. 1991. Some interactions between young walleye pollock and their environment in the western Gulf of Alaska. CalCOFI Rep. 32: 22–40.

SHELTON, P.A., J.E. CARSCADDEN, AND J.M. HOENUG. 1993. Risk evaluation of the 10% harvest rate procedure for capelin in NAFO Division 3l. *In* S.J. Smith, J.J. Hunt, and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120: 193–202.

SHEPHERD, J. (CONVENER) 1991. Special Session on Management under Uncertainties. NAFO Sci. Counc. Studies, 16: 189p.

SMITH, S.J. 1993. Risk evaluation and biological reference points for fisheries management: a review, p. 339–354. *In* G. Kruse, D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II [ed.] Proceedings of the International Symposium of Management Strategies for Exploited Fish Populations. Alaska Sea Grant College Program Report No 93-02, University of Alaska Fairbanks, Fairbanks, Alaska.

SMITH, S.J., J.J. HUNT, AND D. RIVARD (ED.) 1993. Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120. 442 p.

Appendix

The economic submodel tracks two economic sectors, a harvesting and a processing sector. Within a year, each sector operates over two fishing seasons: a spring fishery and a fall fishery. Prices for three products made from pollock are also tracked: surimi, fillets, and roe. Variable names used in the following equations are as follows:

NY	number of years in simulation
i	year index (i = 1,NY)
j	age index (j = 3,10)
h	fishing season index (h = 1,2)
CB_{hj}	catch biomass of j year old pollock from fishing season h
TB_i	total catch biomass in year i
MFB_i	mature female biomass in the population in year i
TPB_i	total population biomass in year i
CS_i	catch biomass turned into surimi in year i
CF_i	catch biomass turned into fillets in year i
CR_i	catch biomass turned into roe in year i
HR_i	total gross revenue from harvesting sector in year i
PR_i	total gross revenues from processing sector in year i
HC_i	total harvesting costs in year i
PC_i	total processing costs in year i
PH_i	annual profits from harvesting sector in year i
PP_i	annual profits from processing sector in year i
TAP_i	total annual profit from both sectors in year i
DVH	present discounted value of harvesting profits
DVP	present discounted value of processing profits
DV	present discounted value of entire fishery
RS_i	total revenue derived from surimi in year i
RF_i	total revenue derived from fillets in year i
RR_i	total revenue derived from roe in year i
EVP	ex-vessel price
VHC	variable harvesting cost
VPC	variable processing costs
BSH	boat share
LRS	length of roe season
DR	discount rate

YS	yield of surimi
YF	yield of fillets
YR	yield of roe
PS	market price of surimi
PF	market price of fillets
PR	market price of roe

Total catch biomass is calculated as the sum of the catch biomass from the two fishing seasons summed over all exploitable ages:

$$TB_i = \sum_{h=1}^{2} \sum_{j=3}^{10} CB_{hj}.$$

The catch biomass converted to surimi products is the sum of the catch from two fishing season components. From the first season only, ages 3 through 8 are included. From the second season, ages 3 through 7 are included. This formulation is based on the assumption that larger, older fish will be turned into premium fillets instead of surimi. In the first season, pollock flesh is soft, so older age groups are converted into surimi:

$$CS_i = \sum_{j=3}^{8} CB_{1j} + \sum_{j=3}^{7} CB_{2j}.$$

The catch biomass converted into fillets is the difference between the total catch biomass minus that part of the total catch converted into surimi. Note that by difference the catch biomass converted into fillets consists of age groups 9 and 10 from the first season and ages 8 through 10 from the second season:

$$CF_i = TB_i - CS_i.$$

The catch biomass converted into roe is the product of the fraction of the total population biomass comprising of mature females times the catch biomass. Note in this formulation that during the spring fishing season, pollock catch biomass is converted into all three products:

$$CR_i = \frac{MFB_i}{TPB_i} \cdot \sum_{j=3}^{10} CB_{1j} \cdot \frac{LRS}{4}.$$

The last term in the above equation corrects for the length of the roe season (3 mo) relative to the duration of the spring fishery (4 mo).

The revenue generated from the various pollock products is calculated as total product biomass multiplied by the yield percentage and the market price:

$$RS_i = CS_i \cdot YS \cdot PS$$

$$RF_i = CF_i \cdot YF \cdot PF$$

$$RR_i = CR_i \cdot YR \cdot PR.$$

Gross revenue to the harvesting sector is calculated as the product of the ex–vessel price of the catch, the total catch biomass, and the boat share percentage:

$$HR_i = EVP \cdot TB_i \cdot BSH.$$

Harvesting sector costs associated with taking the catch are the product of the variable cost parameter and the total catch biomass:

$$HC_i = VHC \cdot TB_i.$$

Gross revenue to the processing sector is calculated as the sum of the revenues generated from the mix of the three pollock products:

$$PR_i = RS_i + RF_i + RR_i.$$

Total processing sector costs are calculated as the product of the variable processing cost parameter multiplied by the sum of the biomass converted to surimi and fillets plus the cost of buying the raw product (catch biomass) from the harvesting sector:

$$PC_i = (VPC \cdot (CS_i \cdot YS) + (CS_i \cdot YF)) + HR_i.$$

Because roe is a byproduct, not a primary product, we assume that the marginal production costs are essentially zero. Thus, there is no term in the above equation related to roe production costs. Note also that revenue to the harvesting sector is considered a cost to the processing sector.

Net returns to the harvesting and processing sectors are the difference between revenues and costs; we ignore the fixed cost component of these sectors:

$$PH_i = HR_i - HC_i$$

$$PP_i = PR_i - PC_i.$$

Annually the total return realized by both sectors is the sum of the returns from each sector:

$$TAP_i = PH_i + PP_i.$$

Harvesting and processing profits discounted and summed for present value are calculated by

$$DVP = \sum_{i=1}^{NY} \frac{1.0}{(1 + DR^{(i-1)})} \cdot PP_i$$

$$DVH = \sum_{i=1}^{NY} \frac{1.0}{(1 + DR^{(i-1)})} \cdot PH_i$$

and the present discounted value of the entire fishery is calculated as

$$DV = DVH + DVP.$$

Use of Gaming Procedures in Evaluation of Management Experiments

Carl Walters

Fisheries Centre, University of British Columbia, Vancouver, BC V6T 1W5, Canada

Walters, C. 1994. Use of gaming procedures in evaluation of management experiments. Can. J. Fish. Aquat. Sci. 51: 2705–2714.

Management often involves debate about whether to maintain some conservative, status quo policy or to experiment with some risky alternative that may produce higher long-term value. In comparing such alternatives, a key modelling problem is to predict the transient response pattern that will occur if an experimental approach is adopted but is not successful (stock collapses or fails to recover, enhancement makes no net conributution to catches, etc.), in terms of how long it will take to detect and react to the failure. Prediction of such transients involves modelling not only future data gathering and statistical analysis, but also how future managers will react to the information. Management gaming involving real managers may be the simplest and most efficient way to make such predictions. Application of gaming procedures to fisheries development and hatchery production examples indicates that such procedures may not only help in prediction, but also are useful for management training and clarification of objectives and priorities.

La gestion implique souvent un débat sur le choix entre le maintien d'un statu quo conservateur et l'aventure d'une alternative risquée qui pourrait donner de meilleurs résultats à long terme. Dans la comparaison de ces options, le problème clé de la modélisation est la prédiction du régime transitoire de réaction qui apparaîtra si on adopte une approche expérimentale qui se solde par un échec (le stock s'effondre ou ne parvient pas à se rétablir, la mise en valeur ne se traduit pas par une contribution nette aux prises, etc.); on cherche à savoir combien de temps il faudra pour détecter l'échec et y réagir. La prédiction de ces régimes transitoires demande une modélisation non seulement de la collecte future et de l'analyse statistique des données, mais aussi de la façon dont les futurs gestionnaires réagiront à l'information. La manière la plus simple et la plus efficace de faire de telles prévisions est peut-être la simulation de gestion avec de vrais gestionnaires. L'application des procédures de jeu à des exemples de développement des pêches et de production aquacole indique que ces méthodes peuvent non seulement aider à la prévision mais être utiles pour la formation des gestionnaires et pour la clarification des objectifs et priorités.

Received November 19, 1993
Accepted October 4, 1994
(J121677)

Reçu le 19 novembre 1993
Accepté le 4 octobre 1994

Fisheries policy development often involves fierce debate between cautious, conservation-oriented interests versus more optimistic, often development-oriented interests. Scientific uncertainty is usually central to such debates, with each side defending whatever hypothesis about stock size or productivity would best serve its policy interests. During fisheries development, debate at each decision point is about whether still larger catches can be sustained; here the cautious view is represented by low estimates of stock size and emphasis on risk assessments related to stock collapse, while the optimistic view is represented by arguments about downward bias in stock size assessments and "black hole" arguments about existence of fishing grounds that have yet to be exploited. Following stock declines, debate often centers on whether very restrictive fishing is needed to allow recovery, with optimistic interests arguing that the decline may not have been due to overfishing in the first place so the decline will reverse itself naturally without any extraordinary management measures. When wild stocks decline in the face of increasing hatchery production, cautious interests might argue either that competition is a problem or that increased fishing pressure (attracted by the hatchery fish) is causing overexploitation, while proponents of the hatchery system might blame the decline on enviromental factors unrelated to the hatchery system.

In such debates, proponents of each view or hypothesis can usually marshall considerable scientific evidence to support that view. Further, the cautious policy alternative is often not informative in the sense that acting as though it were correct would prevent the gathering of critical field experience to test whether another alternative is in fact correct (Walters 1986). Seldom is it possible to resolve the debate simply by investing in more research or monitoring; results of such work can lead to more precise extrapolations about the effects of as yet untested policy alternatives, but cannot in principle eliminate the risks entailed by such extrapolations. Stopping fishery development precludes any direct determination of whether a stock can withstand higher fishing pressure; as noted by Hilborn and Sibert (1988), ultimately the only way to find MSY is to exceed it. Cutting back on fishing after a decline (or hatchery production after a wild stock decline) can be followed by recovery whether the decline was due to overfishing or environment (or hatcheries) in the first place (Skud 1975; Parma and Deriso 1990), leaving us none the wiser about which mechanism was actually responsible (Walters and Collie 1988). In these situations,

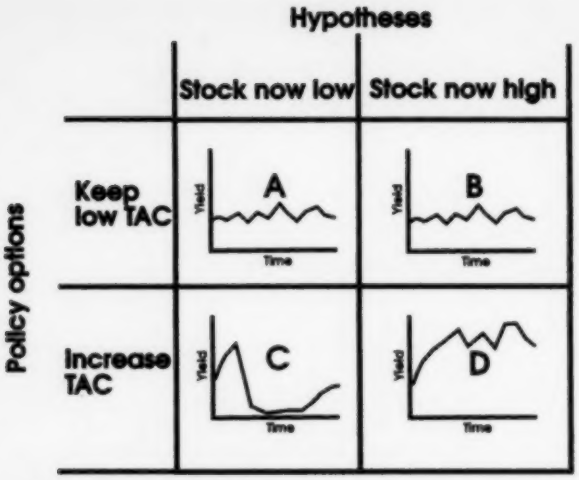


FIG. 1. Graphical decision table showing predicted yield patterns under two policy options during fishery development, for two extreme hypotheses about the current stock size. If allowable catch (TAC) is kept low (cases A and B) the prediction is stable catch whether the stock is large or not. If TAC is increased, there may be either a collapse followed by long-term recovery (case C) or sustained higher catches. The time pattern for case C is particularly difficult to predict, since it depends on how quickly future managers would detect and react to the discovery that high yields are not sustainable.

the key issue for policy debate is not which faction or hypothesis is correct, but rather whether it is "better" for all concerned to adopt a cautious policy (and risk missing an opportunity for improved management), or instead to engage in a more risky management "experiment" (Hilborn et al. 1993). Sometimes it is possible to avoid this difficult choice among risky alternatives by isolating the experimental effects on a few experimental units or pilot test areas, and this obviously makes an experimental approach far more attractive (Walters 1986; Sainsbury 1988; Walters and Collie 1989; McAllister and Peterman 1992a, 1992b).

In principle, management discussions about what risks to take should begin with the construction of a decision tree (e.g. McAllister and Peterman 1992a, 1992b) or decision table (e.g., Walters and Hilborn 1976; Walters 1977; Milliman et al. 1987) like Fig. 1, where scientific hypotheses and policy alternatives are clearly identified and where precise predictions are made about the consequences of each hypothesis–policy possibility. Each row of the table will then portray the range of possible outcomes from applying one of the policy alternatives, and further debate can be focussed on deciding which row is best. Often at least one row of the decision table should represent a cautious or status quo policy, which is robust in the sense that it is expected to produce essentially the same future stream of benefits no matter which hypothesis is correct. The other rows will then represent the outcomes of potentially riskier experimental policies that may have widely varying benefit streams depending on which hypothesis (if any) is correct. At any decision point in time when such a table is constructed, it need not portray a massive or exhaustive comparison of many policies and hypotheses; its main value in the debate is to identify whether there is *any* experimental option worth pursuing in favor of the status quo.

But a fundamental technical difficulty arises in the construction of decision tables such as Fig. 1. Effects of cautious, status quo policies are generally easy to predict, as are the outcomes for table cells where experiments are tried and are successful at improving benefits. The difficult prediction to make is for table cells (policy/hypothesis combinations) representing where an experiment is tried, but turns out to be unsuccessful. This prediction must account for both how long it will take to detect that the policy is not working (a question of statistical and scientific perception) and how future managers would react after detection (questions of flexibility to take corrective actions and management objectives related to avoidance of drastic policy change). In other words, it is necessary to model both future information gathering and analysis and future behavior of analysts and managers. Modelling the statistical performance of experiments is a well-established practice that does not present major conceptual difficulties (e.g., Peterman and Routledge 1983; Collie et al. 1990; McAllister and Peterman 1992a, 1992b). Where really serious trouble arises is in the prediction of how future managers will behave. Most previous research has evaded this troublesome point by assuming that future managers will follow simple decision rules. For example, Walters and Collie (1989), Collie and Walters (1991), and McAllister and Peterman (1992a, 1992b) assumed that designed experimental regimes will be followed for some fixed time period adequate to provide some particular statistical power (probability of choosing correct hypothesis as basis for long term management) and then will follow some feedback rule afterward. In other cases, analysts have attempted to compute the optimum adaptive control policy for future managers to follow, while implicitly assuming that future managers will follow such a policy (Walters and Hilborn 1976; Walters 1981, 1986; Ault and Fox 1989; Parma and Deriso 1990). Both these approaches are clearly too simplistic, and there is a need for ways to better model future management behavior. Walters and Hilborn (1976) suggested that management gaming procedures might provide a useful way to do this modelling.

This paper describes procedures and examples for using management gaming as a way to predict how future managers will respond to the results of management experiments. The essential idea in a gaming approach is that a good predictor of how future managers will behave may be obtained by examining how current managers would behave if faced with various situations that might eventually arise. To conduct this examination, a simulation model is used to generate and present managers with future information patterns like they would see under each alternative hypothesis for stock response, and their reactions (policy responses) to the patterns are recorded. Additional benefits of the gaming activity include training in how to use information more effectively and stimulus to discussion and debate about how to balance various objectives and constraints in making year-to-year policy changes in response to the information.

Gaming Procedures

Computer simulation games have been used in a variety of fisheries contexts, primarily as training tools (Hilborn and

Walters 1986). To be useful for predicting future management behavior, the game must be structured to function efficiently in a relatively complex policy testing environment. In this section, we first suggest one way to organize the gaming environment and then describe components needed for the gaming model. Finally, we note that practical use of the gaming approach involves making a substantial number of trials, which usually must be divided between a "training" set and a policy prediction set, due to the effects of the game itself on the behavior of the people who play future manager roles.

Structure of the Gaming Environment

Figure 2 shows a suggested structure for the gaming environment. The three main components of this environment are (1) an overall control system to present the game-playing manager with a series of gaming trials, to "secretly" select model parameter values (or the hypothesis that the manager will have to deal with) for each game trial, and to record results of multiple trials; (2) a dynamic model that can generate realistic "data" over time for the range of alternative parameter values or hypotheses that are considered consistent with historical experience; and (3) a graphical user interface that allows the game player to quickly review historical and simulated trend data and assessment results in preparation for making each annual gaming decision, and to enter this decision choice efficiently. The next subsection discusses the dynamic model in more detail; this section offers a few suggestions about the control system and interface.

Early gaming applications (e.g., Walters 1977) lacked the overall control system, relying instead on a scientist to carry out the control or "metagame" chores of making secret model choices and recording the player response pattern for each simulation trial. This approach is still helpful occasionally, especially while the interface is being developed and it is not yet clear how to present information most effectively to game players. However, it should be avoided later on, in favor of an automated (computer) selection and recording system, for two obvious reasons. First, there is a tendency for human game controllers to give players "another chance" when they do not perform well under a particular hypothesis, or to choose hypotheses in some systematic order from trial to trial; either of these mistakes leads game players to choose unrealistic decision sequences because they can learn to anticipate which model the controller has chosen. While the central interest in using the game may be only in how future managers will react if an experiment is tried but is not successful, there is no way to be sure that game players will act anything like real future managers if the game players know in advance whether or not the trial they are currently playing will lead to such failure; thus the "secret" choice of hypothesis for each play must be random and independent of previous choices. Second, the decision sequence for each trial is complex to record, and there is a tendency for human controllers to avoid this chore by just recording subjective performance measures such as how long it took the game players to become "confident" about which hypothesis had been chosen for each trial. With a relatively simple automated control system, it is easy both to guarantee an unpredictable hypothesis choice for each trial and to record a variety of decision choice and performance time series for later statistical analysis.

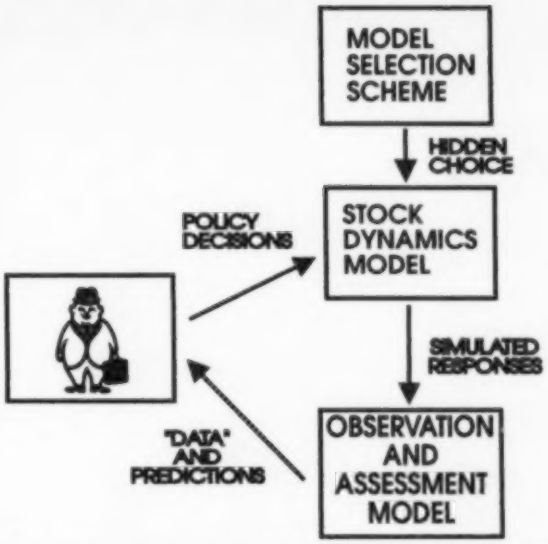


FIG. 2. General components of a management gaming system for assessing the likely responses of future managers to the results of management experiments. This structure can be used to directly make time series predictions for situations like case C in Fig. 1. Human figure in box denotes game player(s); other boxes denote functions performed by computer.

Programming languages like Microsoft's Visual Basic have dramatically simplified the job of constructing graphical user interfaces that allow users to quickly review available data and make policy choices. An example interface arrangement that seems to work well is shown in Fig. 3. This interface has five main parts: (1) a set of master control "buttons" that let players start, end, and review trials; (2) a "policy window" where the user can enter his management decision choice(s) for each simulated year; (3) an "autopolicy window" that allows the user to switch from entering annual decisions to finishing the trial by having the computer follow a prescribed set of decision rules (this option can dramatically speed up the game-playing process by allowing players to avoid entering many repetitive decision choices for later simulation years, after the players are confident about the best policy to follow); (4) a set of "trend summary windows" providing time series graphs as summaries of assessments and performance; and (5) an "assessment window" that provides text and tabular stock assessment results (and management advice) in a relatively detailed format like scientists would normally use to "communicate" with managers.

The assessment window is a particularly critical part of the interface. Without the formal assessment and management suggestions provided in this window, the game player would be left with only trend information and would be forced to either "manage by the seat of his pants" or conduct laborious assessment calculations outside the gaming environment. The first of these alternatives would result in the game being a poor predictor of future management behavior, while the second would preclude doing more than a few gaming trials and would hence greatly increase the risk of obtaining nonrepresentative trial results (chance variation in the simulated data making it either much more or less informative than would be typical or average across many trials).

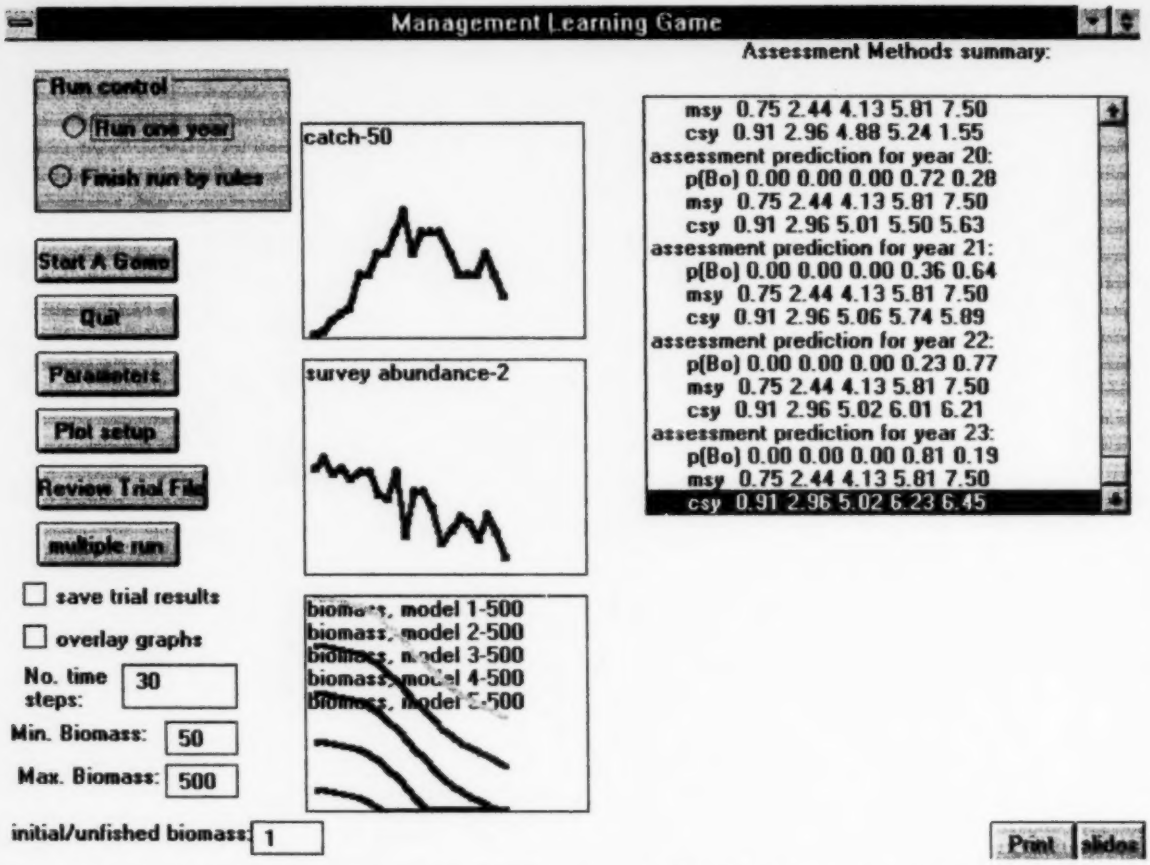


FIG. 3. Sample output display from a management game for development of fisheries on long-lived, unproductive fish species. The game player has allowed catches to increase for about one decade and then has begun cutting back following a few years of low survey abundance estimates. Five curves in bottom panel show the player how survey abundances were predicted to change under five different hypotheses about the initial stock size. The assessment methods summary indicates a high probability (0.81) for the fourth of these hypotheses as of year 23 of play. In this sample, the game player clearly did not react soon enough to evidence of stock depletion.

Gaming Model Components

The gaming model performs three tasks: (1) simulate state dynamics in response to policy choices and to the secret selection of parameter values/hypotheses; (2) generate simulated observations from the state dynamics; and (3) carry out formal assessment calculations (apply assessment methods to the simulated observations, and assign statistical odds to various outcomes). The mathematical modelling and programming chores for tasks (1) and (2) are now familiar to most fisheries scientists who have been involved in the development of stock assessment methods, since these tasks are routinely carried out to generate simulated data for testing assessment procedures. Likewise, most computer schemes for assessment can be embedded within (or called from) a gaming program without major programming difficulties.

There are two quite distinct ways to organize the gaming model components. First, one may use the "operating model" approach (Linhart and Zucchini 1986) where state and observation dynamics are simulated with detailed and realistic submodels for the state and observation dynamics under each alternative hypothesis whereas assessment calculations are done with procedures derived from different (and often much simpler) models. The attractions of this approach are that it provides the game player with simulated data that look very realistic, and also provides insight about possible biases in assessment procedures.

Second, one may use a "parallel predictions" approach, where the state dynamics are simulated simultaneously for all alternative hypotheses, but the game player is provided simulated data and assessment results only from whichever of these simultaneous simulations has been secretly chosen as the correct one. There is an important advantage to this second approach even if it requires that the state dynamics models be simplified somewhat in order to meet computer memory or time constraints: the assessment procedures can be reduced to a simple likelihood/Bayes posterior probability calculation (Walters and Ludwig 1994). This probability calculation is done in two steps: (1) compute the expected values of the observations under each hypothesis, and use the "observed" deviations of the simulated observations from these to estimate the likelihood of obtaining the "observations" given each alternative hypothesis, and (2) calculate an

approximate Bayes posterior probability for each hypothesis as the ratio of its estimated likelihood to the sum of the likelihoods over all the hypotheses (this calculation tacitly assumes that equal prior probabilities are placed on each of the alternative hypotheses).

Besides its computational simplicity and presentation of assessment results in terms of easily interpreted probabilities, the parallel predictions approach offers the attraction of directly representing a way of doing assessment that will likely become much more prevalent in the future. Further, this approach is probably the best way to allay concerns by game players that the game may be too pessimistic because it does not account for potential future advances in assessment methodology; there is in principle no way to extract more information from the data than by using a likelihood/Bayes posterior calculation, except by gathering new kinds of data and/or identifying new hypotheses/models. This raises the interesting question of whether the interface should be designed to allow the game player to gather new kinds of data (by "investing" in new monitoring programs) while each gaming trial proceeds, i.e., should the game be used as a tool for identifying better monitoring designs, at the same time that it is being used to help predict how future managers would respond under various alternative hypotheses? I can only offer an instinctive response to this question, based on experience watching students and managers play fisheries games: I advise caution about asking too much of the game and the players during any one gaming trial, and would try to avoid making the game too open-ended in terms of information gathering. It may well be worthwhile to run sets of trials with different types of information available during each set, but such tests should be kept separate from trials aimed at answering specific questions such as "how long would it probably take to detect whether a particular experimental policy is failing, given the types of data now being collected?"

Training and Performance Trials

It is not generally wise to treat the first gaming trial results as representative or predictive of likely future management behavior. In my experience, most game players will exhibit a learning pattern that reflects both improved understanding of the particular definitions and options contained in the interface, and also better understanding of basic population dynamics relationships and the temporal patterns expected from such relationships (i.e., of both the particular model structure and the broader "principles" that it attempts to represent). I have noticed that even experienced fishery managers often tend at first to (1) overreact to apparent state variations caused by measurement errors (place too much weight on single observations); (2) "probe" the simulated system with impractically large policy changes (because there is no real cost in doing so); and (3) fail to account for time lags when interpreting simulated responses (e.g., expect recruitment to increase immediately after an increase in spawning stock, even in cases where recruits are not seen until they are several years old).

In my experience, it usually takes relatively few "learning trials" before game players stop making obvious mistakes. Five to ten trials generally suffice, representing one or two simulation runs under each hypothesis being considered. Some players will continue to "fine-tune" their reactions after even 20–30 trials, but the effects of such behavior on assessments of average performance across trials are likely to be small relative to the effects of unpredictable variations caused by observation errors and stochastic model components (e.g., environmental effects on recruitment).

Careful observation of game-playing behavior during learning trials is important not only to make sure that trial results are reasonable predictors of future behavior, but also to insure that the game is not overly optimistic about future management performance in discriminating among alternative hypotheses. The game will lead to underestimates of the time required to disciminate among alternatives if either (1) it represents too few alternative hypotheses (only a few distinctive temporal patterns that players can easily learn to recognise); (2) simulated observations are unrealistically precise; and/or (3) the game player is provided with types of observations that would not actually be practical to gather (e.g., accurate estimates of current stock size). Fortunately, such flaws in a game are usually easy to recognise, and correct, after a few gaming trials.

Examples

This section reviews two relatively simple games that illustrate the modelling and interface design approaches discussed above. One game is intended to assist in risk assessments during fishery development for long-lived species, where a key issue is whether good stock size estimates can be obtained early enough to avoid overfishing and a long, painful recovery period. The second has been used to examine alternative policies for experimentally changing hatchery releases of coho salmon (*Oncorhynchus kisutch*), to determine whether hatchery coho have deleterious effects on marine survival rates of wild coho stocks.

Fishery Development for a Long-lived Species

Slow growing, very long-lived, and highly aggregated fish species such as the orange roughy (*Hoplostethus atlanticus*) of New Zealand or the Pacific ocean perch (*Sebastes alutus*) of Canada have proven to be nightmares for fishery managers. On the one hand, these species can produce highly lucrative short-term catches from high accumulated stock biomasses. But on the other, they are likely to produce only very modest long-term yields. Bitter conflicts between biologists and fishermen have characterized the development of fisheries for such species, and management prescriptions have ranged from cautious policies for harvest reduction derived from risk assessment methods (Francis 1992) to experimental depletion policies with relatively high risks of causing overfishing (Walters and Collie 1989). The key issue in stock assessment for these species is not whether the long-term catch is low (that is well recognised), but rather how large is the initial stock size and hence the transient catches that could be taken during fishery development.

Traditional catch–effort methods are not helpful in dealing with this issue because the stocks are far from equilibrium during the development and commercial cpue provides little information about changes in abundance. Risk assessments like Francis (1992) have been used largely to answer "open loop" (no feedback, Walters 1986) questions of the form "if we allow a quota of X for Y years, what is the probability that the stock will be reduced to below Z% of its unfished level?". Experimental design calculations like Walters and Collie (1989) have looked at information gathering

during development, by trying to answer questions like "if we allow an experimental quota of X, how many years will it take us to accurately estimate the unfished stock size, and how likely are we to obtain and use this estimate before the stock is reduced to below $Z\%$ of its unfished level?". But even these design calculations fail to accurately portray how managers may behave to avoid overfishing as information progressively becomes available during the development.

In several cases, direct biomass surveys have been used instead of cpue to provide indices of stock trend. But the total biomass estimates from these surveys are suspect due to uncertainty about how to convert survey densities (catch per swept area, acoustic count) to absolute biomasses (i.e., survey catchability is highly uncertain), and about abundances outside the surveyed areas. Thus the surveys are properly viewed as measures of change in relative rather than absolute abundance. Relative abundance changes are then used in conjunction with estimates of absolute removals (catches) to estimate initial abundance (or place odds on different possible values of initial abundance); these are essentially generalized depletion estimation methods (Hilborn and Walters 1992), where population dynamics models are used to predict corrections during the depletion for effects of growth, recruitment, and natural mortality. A key point is that no matter how sophisticated a model is used to apply such corrections, the accuracy of the depletion estimators of initial biomass depends critically on the absolute removals being large enough to cause a clear depletion "signal" in the survey abundance indices (Hilborn and Walters 1992).

Thus the manager of a long-lived species is forced into a particularly difficult decision position. On the one hand, he should recommend low catches to avoid overexploitation (and economic overcapitalization during the development); but on the other hand, he can only obtain good stock size estimates (given available survey technology) by allowing higher catches. By allowing higher catches early in development, he can reduce the "legacy of uncertainty" to be borne by future managers and fishermen, but in doing so he also increases the risk that they will have nothing left to catch. This fundamental conflict or trade-off between protection and information gathering objectives is an example of the "dual effect of control", which creates major computational problems for any analyst who seeks to assess an optimum stochastic control policy (Walters 1986). It is simply nonsense to assert that managers can effectively find the best place to be along such trade-offs by applying simplistic prescriptions such as "always err on the conservative side". Gaming can obviously help both to see the trade-off relationship more clearly (to see how early catches affect assessment estimation performance), and to find compromise policies.

For this example, the gaming interface (Fig. 3) and model structure need not be very complex. Basically, the game manager needs to see three types of information: trends in catch and survey index abundance, and depletion estimation results for initial abundance. Each year he makes a single decision (the allowable catch or quota). The alternative hypotheses are a set or grid of different values for the unfished stock size (where each unfished stock size also implies a different average recruitment rate needed to have sustained it before fishing began). For game playing on the typical time scale of fishery development (10–30 yr), the dynamic model needs to account for age structure (for this example, I used the model structure described in Francis 1992) but might not even include a stock–recruitment relationship, since most of the recruitment that will occur during the development has already happened (is in place in the prerecruit age structure). However, I recommend including the stock–recruitment relationship (with stochastic environmental effects), to permit flexibility for game players to examine longer term scenarios for depletion and stock rebuilding.

Three striking patterns quickly become evident when this game is played. First, in my experience, even quite cautious biologists tend to "probe" the system too hard to obtain information in the first few simulation years, until they have done enough game trials to have caused a few stock collapses; they then begin to search actively for less risky compromise policies.

Second, it has so far been difficult or impossible to reach concensus among game players about two issues or questions related to management objectives: (1) how large an overrun of MSY (or initial "overcapitalization" for short-term profit) should be permitted during development, even within the range of overrun values that do not lead to high risks of stock collapse, and (2) what is an acceptable probability of stock collapse, measured for example by the probability of reducing the stock to less than one half of its virgin biomass within a 30-yr gaming period. Presumably the difficulty in reaching concensus reflects high variation among game players in personal preferences regarding both incomes over time and risk taking. It also becomes obvious very early in debates about these questions that fisheries managers have been provided woefully little guidance about what standards might best serve the "public" interest.

Third, the ability to make quota changes as new information becomes available has a profound effect on recommendations about what quotas can be safely taken early in development. Figure 4 shows the results of 200 simulation trials. For the first 100 trials, the gaming system was used to mimic a simple risk assessment: quotas were fixed at nine different levels (20 trials per level) for the entire simulation period. Obviously, the probability of causing a stock collapse (to less than one half virgin within 30 yr) increases with the quota, and from these results one might conclude that initial quotas above 10 thousand tons are unacceptably risky. For the second 100 trials, game players (author and 10 students) were asked to initially allow progressively higher quotas (same starting values as first 100 trials) for at least 2 yr, but were then encouraged to vary the quota over time in response to modelled assessment results. Not surprisingly, they were generally able to drastically reduce the probability of collapse for intermediate initial quotas (5–20 thousand tons), suggesting that "safe" initial quotas (to have the same probability of collapse as for nonadaptive simulations) are at least double what would be predicted from the simpler risk assessment. Such striking results do not imply that high initial quotas are always a wise choice in terms of social and economic objectives, especially since they are followed in most trials by drastic and rapid quota reductions later on; but they do indicate that debate about biological risks can be resolved through gaming tests, leaving decision makers to focus on the much more difficult issue of whether large quota changes are acceptable in terms of socioeconomic objectives.

Testing for Effects of Hatchery Production on Wild Stocks

This example illustrates the use of gaming in a much more complex policy and scientific environment, the management of Pacific salmon. This management involves harvest regulation, hatchery production, and habitat protection for a vast complex of stocks, and there are great scientific uncertainties about all aspects of the system. Here I will focus on a restricted case area where some key issues and uncertainties have become particularly plain.

The Strait of Georgia in southern British Columbia supports one of Canada's most valuable recreational fisheries, for chinook (*Oncorhynchus tshawytscha*) and coho salmon (Argue et al. 1983). Over a hundred streams around the Strait (and Puget Sound to the south) contribute wild juveniles to the system (Walters and Cahoon 1985), and a high proportion of these fish spend their ocean rearing period within the Strait. To "supplement" natural production in the face of growing fishing pressure, the Canadian Department of Fisheries and Oceans (DFO) began a large hatchery production program in the early 1970's, which achieved peak releases of over 10 million coho smolts and 27 million chinook fry and smolts by the mid-1980's; at present, these hatchery fish make up nearly half the coho catch and around 20% of the chinook catch (Cross et al. 1991). To our surprise, this program has not doubled salmon catches as expected; coho catch has fluctuated without any noticeable trend, and chinook catch has actually declined dramatically. Marine survival data from coded wire tagging (CWT) programs indicate that the proximate reason for this "failure" could be declines in marine survival rates of both wild and hatchery fish (Cross et al. 1991; Walters 1993). Very similar patterns of declining marine survival in the face of increasing hatchery releases occurred about a decade earlier off the Oregon coast, and have stimulated much debate about the possibility of density dependence in survival rates (Nickelson 1986; Emlen et al. 1990). However, such marine survival trends can also be explained by hypotheses involving changes in oceanographic factors (e.g., temperature, marine pollution in the Strait of Georgia). An experimental approach to distinguishing between the density-dependence and oceanographic factor hypotheses, by manipulating hatchery smolt releases, has been suggested (Peterman and Routledge 1983; Peterman 1991).

Since total catch in the Strait of Georgia has not increased, but catch of hatchery fish has, it obviously follows that catches of wild fish have decreased substantially. Although spawning escapements of chinook and coho have been very poorly monitored, various escapement indices (fishery officer counts, fence counts for a few streams) also indicate a wild stock decline. In 1990 and 1991, planning documents for coho (Anonymous 1990, 1991) expressed alarm at this decline and suggested various policy options for reversing it. These documents attributed the decline in marine survival rates to poor performance at only a few hatcheries, and blamed the catch/escapement declines entirely on freshwater habitat loss and overfishing; reductions in hatchery releases were not mentioned as a possible solution for the problem. The importance of protecting and restoring habitat was mentioned, but the documents focussed mainly on regulations to reduce annual coho exploitation rates from the 80% levels indicated by CWT returns to around 70%, a level that various stock–recruitment assessments suggest might be near optimum for many coho stocks. However, I noted

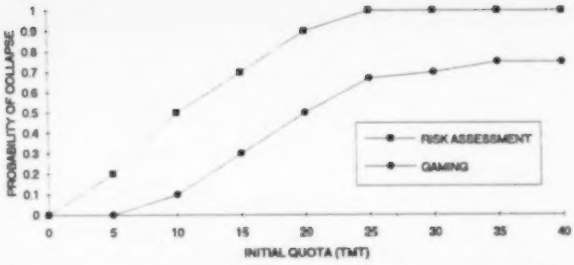


FIG. 4. Summary of results from many gaming trials using the interface in Fig. 3, compared with simpler risk assessment predictions. Experienced game players have a much lower probability of causing a stock collapse (reducing stock to less than 20% of unfished level), even after starting with high initial quotas, than would be predicted by risk assessments that ignore future management adjustments as new information becomes available.

(Walters 1993) that backcalculation of wild smolt numbers from CWT survival data and catch data would suggest that wild coho smolt numbers have not declined since the early 1970's (wild catch + escapement would have declined by more than 50% if marine survival had declined by that much and smolt numbers had also decreased), and if smolt numbers have remained high, then neither overfishing nor habitat loss could be to blame for the problem. The response to this challenge was that there are few CWT survival estimates for wild stocks, and these may not be representative.

DFO biologists suggested development of a management game that could represent all four alternative hypotheses (marine density dependence, marine environment trends, freshwater habitat loss, overfishing) and make predictions for each alternative about how total catches, wild stock catch contributions, and CWT marine survival indices should behave in the future under various harvest regulation and hatchery production options. A particular objective for this game would be to help determine how long it might take to distinguish between the marine density-dependence and oceanographic trend hypotheses, and what losses might be suffered by the fishery, if hatchery releases were varied up and down in alternating years to create a density pattern unlikely to be correlated with any environmental patterns that might occur in the next few decades.

Perhaps the most difficult technical problem in developing a simulation game for a complex situation such as this is in deciding what to leave out of the calculations. Should we include dozens of separate hatchery and wild stocks that are known to have distinctive biologies and for which historical data are available, or should we lump the calculations into total wild and hatchery components? Should we follow survival and exploitation patterns on very short time steps of a week or two (as in Argue et al. 1983), so as to account for seasonal details of the exploitation process and allow exploration of particular regulatory options such as seasonal closures and bag limits, or should we instead allow the user to vary only overall exploitation rates? Should we propose and model specific, detailed mechanisms for the marine density-dependence hypothesis (in terms of factors such as juvenile spatial distributions, food competition and growth bioenergetics, and possible impacts of particular predators), or should we instead use a simple relationship between total smolts and total survival rate? In my experience,

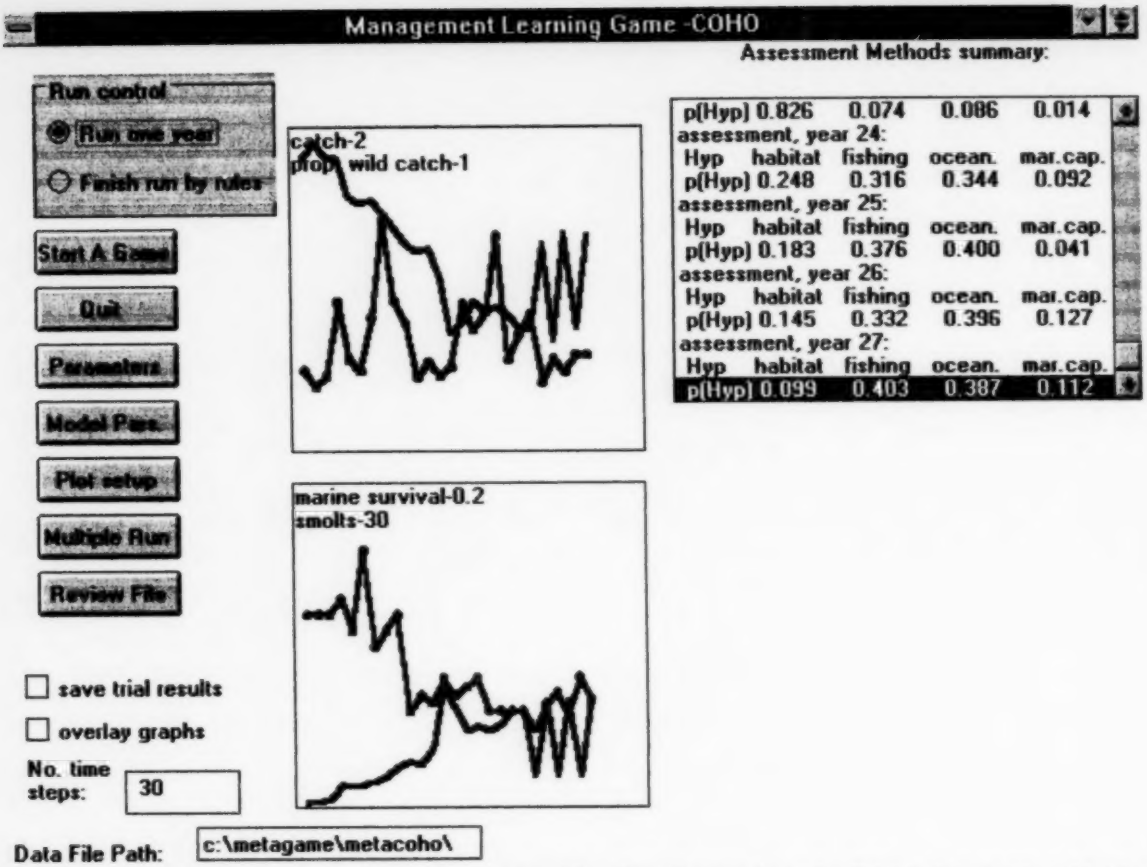


FIG. 5. Sample output display from a gaming interface for examining alternative experimental policies for harvest rate and hatchery release manipulation to rebuild wild coho salmon stocks in the Strait of Georgia, B.C. Top graph panel shows historical decline in proportion of wild coho in the catch, and lack of trend in total catch; final 8 yr show simulated trends in these indices under a policy where exploitation rate was reduced (from 0.8 to 0.7) and hatchery releases were varied from 3 million to 10 million smolts in alternate years. Bottom graph panel shows historical and simulated changes in marine survival rate (declining over time) and hatchery releases (increasing historically then fluctuating under the experimental regime). Assessment methods summary shows that the experimental results to date do not clearly favor any of the four major hypotheses for decline, although the correct one (overfishing in this particular trial) is beginning to look most probable.

the best rule to use in answering such questions is to be as parsimonious as possible: keep referring back to the basic objectives for developing the model, and add no complications that are not absolutely necessary to meet those. In the end, we decided to use a quite simple biological model, and to allow only general hatchery and harvest policy interventions (total smolt releases, regulation of total exploitation rates and proportions of wild fish retained in the catch). Given policy results based on these general interventions, a variety of more detailed models are already available to examine specific regulatory packages for achieving such results. Likewise, modelling many stocks and detailed biological responses is an invitation to massive compounding of errors due to the large number of parameters that would have to be estimated.

For all hypotheses, we decided that the game should account for the following three basic relationships: (1) the spawner to smolt "stock–recruitment" relationship for wild stocks, thought to be hyperbolic (Beverton–Holt form) with an initial slope representing good survival at low rearing densities (but not steep enough to fully seed the freshwater rearing environment under the overfishing hypothesis) and an asymptote representing habitat carrying capacity (decreasing over time under the habitat loss hypothesis); (2) marine survival rate, varying inversely with combined hatchery plus wild smolt density under the density-dependence hypothesis but simply decreasing without linkage to density under the oceanographic factor hypothesis; and (3) a direct relationship between harvestable abundance (smolts × marine survival) and fishing effort, representing particularly how sport fishing responds rapidly to changes in the total number of fish available (Argue et al. 1983). Coding these relationships into a simulation, with appropriate accounting for time delays, etc., turned out to be largely a routine task.

Parameter estimates that would give realistic simulation results were available from a variety of previous assessments such as Argue et al. (1983). Recent DFO work on computerized stream habitat inventories, and estimates of historical rearing densities (Marshall and Britton 1990), were particularly critical in setting up the spawner–smolt

relationship. The only major conceptual difficulty encountered during during development of the model was in deciding how to parameterize the habitat loss hypothesis: habitat loss obviously affects freswhater carrying capacity (maximum smolt production), but does it also affect maximum egg–smolt survival rates at low spawner densities (and hence susceptibility to recruitment overfishing)? In the end, we elected to be conservative and assume both effects, implying that the main distinction between the overfishing and habitat hypotheses is in predicted response to reduced fishing (increased spawning), with the habitat loss hypothesis predicting only minor recovery.

Presumably, future discrimination among these hypotheses will involve a combination of informed judgement based on trends in various indicators (catch, survival, etc.), along with formal probability assessments using likelihood functions for the various kinds of observations. By using the parallel predictions approach described above, it was a simple matter to provide game players with a crude Bayesian probability calculation for each simulated year, along with graphical displays of trends. This calculation was just the relative likelihood of all the data (catches, proportion of wild fish in catches, marine survival rates) up to that year for each hypothesis (with likelihood components calculated using the same probability densities as used to generate stochastic variation in model observations), divided by the sum of such relative likelihoods over all hypotheses. To provide a "level playing field" for all four hypotheses, historical data were excluded from this likelihood calculation (otherwise, only the two marine survival hypotheses would be assigned high probabilities at the start of each game play). Marine survival rate "observations" were generated with a variance twice as large as indicated by historical data, to reflect distrust by DFO biologists in assessments based on trends in marine survival rate. This arbitrary choice forces the game to be very conservative in its predictions of how long it would take to detect effects of variation in hatchery releases under the marine carrying capacity hypothesis.

Essentially the same gaming interface was used as for the fishery development example, with a somewhat more complex graphical display and more windows to represent policy interventions (Fig. 5). A single play of this game, making annual hatchery stocking rate and fishing regulation decisions for 30 yr, requires a minimum time of about 5 min. To speed up the play for multiple trials aimed at estimating power of alternative experimental designs, we decided to include an "autorun" option that lets the game player specify a fixed experimental schedule for a block of years (e.g., hold exploitation rate constant at 75% for 10 yr, while varying hatchery releases between 2 and 10 million smolts in alternating years) and then look at the results from this block before proceeding or ending the trial. Players have ended up using mainly this autorun option, with experimental time blocks of 6–10 yr.

Perhaps the most important result from this game to date (with limited play by four biologists and three graduate students) has been a clear appreciation of the need for very long-term management strategies and experimental programs. Most players enter the game expecting to see useful results within a few years. But harvest rate reductions take at least 3 yr (coho life cycle) to even begin to bear fruit, and many more years before trends predicted by the overfishing and habitat hypotheses become evident in the face of natural variation in productivity. Even substantial reductions (50–80%) in hatchery releases do not result in clear patterns of variation in marine survival rate until several years of alternating low and high releases are available for comparison.

Another lesson from this game is the importance of choosing between a harsh experimental regime that will produce clear answers, versus doing nothing at all. Game players that try modest experiments in an effort to avoid risk (such as reducing hatchery releases by only 20–30% in alternating years) soon discover that they cannot detect corresponding marine survival rate changes under the carrying capacity hypothesis (in the face of assumed random variation in these rates), at least within the 30-yr trial period allowed. Yet they can incur significant losses in cumulative catch under the marine environment and habitat loss hypotheses. (Weak hatchery release experiments do produce some benefits to wild stocks under the overfishing hypothesis, through reduced fishing effort in years when hatchery fish are less abundant.)

It remains to be seen whether decision makers for the Strait of Georgia will view the potential for lost catches associated with doing a relatively harsh hatchery manipulation experiment as being a lesser risk than the loss of wild production if the carrying capacity hypothesis proves correct. But the game has indicated that this difficult choice should be made, and soon: it seems that the worst policy choices today are to do nothing (leave the uncertainty unresolved unless the marine environment hypothesis is correct), or to arbitrarily discontinue hatchery production entirely so as to save wild stocks. Currently, a "drastic" manipulation of hatchery releases is actually coming to be seen as a moderate compromise between such policy extremes, rather than as an extreme in itself.

Discussion

The examples presented above have obviously not been chosen to convince decision makers that management gaming will make their lives easier by speeding the discovery of sound management prescriptions. Indeed, game playing often forces very difficult decision choices about risk taking out into the open, exposing the hazards of both inaction (do nothing and hope the problem goes away) and reliance on simplistic decision rules. It also exposes the silliness of arguments about postponing decisions until "all the facts are available", by pointing out through simulated data gathering that such facts generally do not become available (if ever) until well after the decision is actually tried.

As scientists, we can (and probably will) quibble endlessly about precisely how to model particular alternative hypotheses, how to do the most realistic probabilistic calculations in generating fake data, what assessment methods best reflect future options that managers will have, how many alternative hypotheses to include in games, and so forth. Luckily, the most important insights to be had from gaming models (about policy alternatives and trade-offs) can be made evident even with very crude calculations. It is obviously critical to include a wide enough range and large enough number of hypotheses to fairly represent the main domain of scientific uncertainty, and to present simulated observations with enough noise to avoid misleading game players about how rapidly learning can take place. But within such limits, we have wide latitude. For instance, essentially the same conclusions about risk and overdevelopment would

be evident from simple surplus production models as were obtained above with an age-structured calculation. Likewise, inclusion of many more alternative hypotheses about possible oceanographic trends and effects on survival would not alter the basic conclusion that an experimental regime of hatchery releases is an important way to guard against confusion of oceanographic with density-dependent effects.

This paper began with a suggestion that gaming is particularly useful as a way to predict how long it should take to detect failure in experimental management regimes. In the fishery development example, this prediction was presented as a change in the harvest that should be obtained without an increase in risk compared with what would be predicted from a nonadaptive calculation (Fig. 4). In the hatchery example, it was presented in terms of a discouraging indication that reduced harvest rates can take decades to bear fruit, and even violent hatchery release manipulations may take up to a decade to provide clear answers. I have not attempted in either case to cast the gaming results in the format of a formal decision table; to do so would require far more precise definitions of management success/failure measures and objectives than are needed to demonstrate the methodology. Indeed, it is not entirely clear that fisheries scientists will ever be able to carry out that last step (decision table) with much credibility or success at influencing decision making, due to difficulties in obtaining concensus about how to weight various performance measures and time preferences. But we can at least use gaming to help point the way toward policies that represent wise compromises, and more clearly expose those trade-offs that are worthy of deeper thought and debate.

Acknowledgements

I am grateful to the colleagues and students who have acted as test managers for gaming trials, especially E.A. Perry (DFO, Vancouver) and Scot Mountain (UBC). Thanks to Laura Richards and Bernard Megrey for allowing me to talk about the ideas at AFS Portland, where discussions with many people helped greatly in formulating this paper. Randall Peterman and an anonymous reviewer made many helpful comments on the manuscript. Financial support was provided by a DFO contract and by NSERC operating grant A5869.

References

ANONYMOUS. 1990. Coho resource status and management planning process, interim report. Department of Fisheries and Oceans, Pacific Region, Vancouver, B.C. 70 p.

ANONYMOUS. 1991. Coho resource status and management planning proposal. Department of Fisheries and Oceans, Pacific Region, Vancouver, B.C. 22 p.

ARGUE, A.W., R. HILBORN, R.M. PETERMAN, M.J. STALEY, AND C.J. WALTERS. 1983. Strait of Georgia chinook and coho fishery. Can. Bull. Fish. Aquat. Sci. 211: 91 p.

AULT, J.S., AND W.W. FOX JR. 1989. FINMAN: simulated decision analysis with multiple objectives. Am. Fish. Soc. Symp. 6: 166–179.

COLLIE, J.S., R.M. PETERMAN, AND C.J. WALTERS. 1990. Experimental harvest policies for a mixed-stock fishery: Fraser River sockeye salmon, *Oncorhynchus nerka*. Can. J. Fish. Aquat. Sci. 47: 145–155.

COLLIE, J.S., AND C.J. WALTERS. 1991. Adaptive management of spatially replicated groundfish populations. Can. J. Fish. Aquat. Sci. 48: 1273–1284.

CROSS, C.L., L. LAPI, AND E.A. PERRY. 1991. Production of chinook and coho salmon from British Columbia hatcheries, 1971 through 1989. Can. Tech. Rep. Fish. Aquat. Sci. 1816: 48 p.

EMLEN, J.M., R.R. REISENBICHLER, A.M. MCGIE, AND T.E. NICKELSON. 1990. Density-dependence at sea for coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 47: 1765–1772.

FRANCIS, R.I.C.C. 1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. Can. J. Fish. Aquat. Sci. 49: 922–930.

HILBORN, R., E.K. PIKITCH, AND R.C. FRANCIS. 1993. Current trends in including risk and uncertainty in stock assessment and harvest decisions. Can. J. Fish. Aquat. Sci. 50: 874–880.

HILBORN, R., AND J. SIBERT. 1988. Adaptive management of developing fisheries. Mar. Policy 12: 112–122.

HILBORN, R., AND C.J. WALTERS. 1986. Microcomputer fisheries simulations as training and teaching tools. Environ. Software 1: 156–163.

HILBORN, R., AND C.J. WALTERS. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York, N.Y. 570 p.

LINHART, H., AND W. ZUCCHINI. 1986. Model selection. John Wiley and Sons, New York, N.Y. 429 p

MARSHALL, D.E., AND E.W. BRITTON. 1990. Carrying capacity of coho streams. Can. MS Rep. Fish. Aquat. Sci. 2058: 39 p.

MCALLISTER, M.K., AND R.M. PETERMAN. 1992a. Statistical analysis of a large-scale fishing experiment designed to test for a genetic effect of size-selective fishing on British Columbia pink salmon (*Oncorhynchus gorbuscha*). Can. J. Fish. Aquat. Sci. 49: 1305–1314.

MCALLISTER, M.K., AND R.M. PETERMAN. 1992b. Experimental design in the management of fisheries: a review. N. Am. J. Fish. Manage. 12: 1–18.

MILLIMAN, S.R., A.P. GRIMA, AND C.J. WALTERS. 1987. Policy making within an adaptive management framework, with an application to lake trout (*Salvelinus namaycush*) management. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 425–430.

NICKELSON, T.E. 1986. Influence of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. Can. J. Fish. Aquat. Sci. 43: 527–535.

PARMA, A.M., AND R.B. DERISO. 1990. Experimental harvesting of cyclic stocks in the face of alternative recruitment hypotheses. Can. J. Fish. Aquat. Sci. 47: 595–610.

PETERMAN, R.M. 1991. Density-dependent marine processes in Pacific salmonids: lessons for experimental design of large-scale manipulations of fish stocks, p. 69–77. *In* S. Lockwood [ed.] The ecology and management aspects of extensive aquaculture. International Council for the Exploration of the Sea, Marine Science Symposium 192, Copenhagen.

PETERMAN, R.M., AND D.M. ROUTLEDGE. 1983. Experimental management of Oregon coho salmon: designing for yield of information. Can. J. Fish. Aquat. Sci. 40: 1212–1223.

SAINSBURY, K.J. 1988. The ecological basis of multispecies fisheries and management of a demersal fishery in tropical Australia, p. 349–382. *In* J.A. Gulland [ed.] Fish population dynamics, 2nd ed. John Wiley and Sons, New York, N.Y.

SKUD, B.E. 1975. Revised estimates of halibut abundance and the Thompson–Burkenroad debate. Int. Pac. Halibut Comm. Sci. Rep. 56: 35 p.

WALTERS, C.J. 1977. Management under uncertainty, p. 261–297. *In* D.V. Ellis [ed.] Pacific salmon: management for people. Western Geographic Series, Vol. 13. University of Victoria, Victoria, B.C.

WALTERS, C.J. 1981. Optimum escapements in the face of alternative recruitment hypotheses. Can. J. Fish. Aquat. Sci. 38: 679–689.

WALTERS, C.J. 1986. Adaptive management of renewable resources. McGraw Hill Publ. Co., New York, N.Y. 386 p.

WALTERS, C.J. 1993. Where have all the coho gone? British Columbia Association of Professional Biologists/American Fisheries Society Symposium on Wild and Enhanced Coho Stocks, Proceedings.

WALTERS, C.J., AND P. CAHOON. 1985. Evidence of decreasing spatial diversity in British Columbia salmon stocks. Can. J. Fish. Aquat. Sci. 42: 1033–1037.

WALTERS, C.J., AND J.S. COLLIE. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45: 1848–1854.

WALTERS, C.J., AND J.S. COLLIE. 1989. An experimental strategy for groundfish management in the face of large uncertainty about stock size and production, p. 13–25. *In* R.J. Beamish and G.A. McFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. 108.

WALTERS, C.J., AND R. HILBORN. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33: 145–159.

WALTERS, C., AND D. LUDWIG. 1994. Calculation of Bayes posterior probability distributions for key population parameters. Can. J. Fish. Aquat. Sci. 51: 713–722.

Uncertainty and Risk Evaluation in Stock Assessment Advice for U.S. Marine Fisheries

Andrew A. Rosenberg

National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02540, USA

and Victor R. Restrepo

University of Miami, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

Rosenberg, A.A., and V.R. Restrepo. 1994. Uncertainty and risk evaluation in stock assessment advice for U.S. marine fisheries. Can. J. Fish. Aquat. Sci. 51: 2715–2720.

This paper describes some of the ways that the uncertainty in fisheries scientific advice has been communicated to managers for different fisheries in the United States in the past several years. Describing the uncertainty can be important in allowing managers to weigh the benefits and losses of different management strategies and to allay concerns about the effects of process, measurement, and model errors on the scientific advice, even if a formal decision theoretic risk analysis has not been carried out. The four general steps in analyzing uncertainty and assessing risk are estimation of the uncertainty in the assessment of current stock status due to measurement error, evaluation of the impacts of potential model errors on the assessment, stochastic projections incorporating estimation error and process errors to investigate the impacts of different management options, and assessment of risk using simple utility functions. At least one of these steps has been included in assessment analyses of about 20 major U.S. fisheries. All of these steps have been incorporated in the scientific advice on a few fisheries to date and should be attempted whenever possible to improve the information available to fishery managers.

On décrit certaines des manières dont les incertitudes dans les avis scientifiques en matières de pêche ont été communiquées aux gestionnaires pour différentes pêches des États-Unis au cours des dernières années. La description des incertitudes peut être importante pour les gestionnaires qui ont à évaluer les avantages et les pertes associés aux diverses stratégies de gestion possibles et à dissiper les inquiétudes relatives à l'impact sur les avis scientifiques de l'erreur inhérente à la méthode, aux mesures et à la modélisation, et ce même quand une analyse théorique formelle des risques n'a pas été effectuée en vue de la prise de décision. Les quatre grandes étapes à suivre dans l'analyse des incertitudes et l'évaluation des risques sont les suivantes : estimation de l'incertitude dans l'évaluation de l'état actuel des stocks liée à l'erreur inhérente aux mesures, évaluation des impacts des erreurs possibles de modélisation sur l'évaluation, établissement de prévisions stochastiques prenant en compte l'erreur dans l'estimation et l'erreur attribuable à la méthode en vue de déterminer les impacts des diverses options de gestion et évaluation des risques au moyen de fonctions d'utilité simples. Au moins une de ces étapes a été suivie dans les évaluations d'une vingtaine de pêches importantes des États-Unis. À ce jour, les quatre étapes n'ont été suivies dans le processus de formulation des avis scientifiques que pour quelques pêches seulement; on devrait autant que possible veiller à les suivre toutes de façon à enrichir les informations à partir desquelles les gestionnaires des pêches prennent leurs décisions.

Received March 2, 1994
Accepted October 4, 1994
(J12299)

Reçu le 2 mars 1994
Accepté le 4 octobre 1994

As stock assessment methodology has moved toward statistical procedures, increasing attention has been focussed on estimating the uncertainty in assessment advice (e.g., Shepherd 1991; ICES 1993; Smith et al. 1993). It has become routine in many assessments to estimate the variance or distribution of the estimated stock abundance or fishing mortality rate, but in many cases this additional information is primarily used by scientists as a statistical diagnostic for the analysis. Expressing assessment uncertainty to managers is another matter, however, and there is, as yet, no standard approach in the presentation of advice with respect to uncertainty and risk, although several approaches have been suggested (e.g., Francis 1992; Restrepo et al. 1992; Hilborn et al. 1993). Nevertheless, estimates of the uncertainty in the assessment estimates have become part of the advice in all of the regions of the United States for some fish stocks. This is an important step because it is clear to scientists, managers, and the public that uncertainty is a real feature of the status of fish stocks and the scientific advice concerning their management.

Statements concerning the variability of the environment and the unpredictability of stock abundance abound both in public meetings and in the scientific literature (e.g., see Getz et al. 1987; Ludwig et al. 1993). In many cases, a false dichotomy is made between the effects of the environment and the impact of fishing working through the relationship between spawning stock and recruitment. Both effects are important and determining which dominates is rarely a useful distinction. However, for the purposes of giving advice to managers on the status of the resource and its likely

future condition under different harvesting strategies, uncertainty and the stochastic nature of stock dynamics must be incorporated. Similarly, the quality of the data for analysis of stock status is almost invariably an issue in the debate over management actions. Although in many cases the data series are short and noisy or other problems can be identified, there may be little that can be done to improve the situation, especially in retrospect.

Model assumptions present a similar problem. In order to improve the credibility of the scientific advice and provide better information to managers, we need to include the measurement error explicitly, including sensitivity to model assumptions, as a part of the analysis. An important benefit of taking this additional step in an assessment is that it may short-circuit much of the debate over the scientific advice and move to a discussion of management options. In other words, the debate concerning the correct value of the natural mortality rate or the quality of the survey data points can be eased by including other possible values in the analysis of uncertainty. In many cases an uncertainty analysis may show that the recommendation or resultant advice concerning stock status is insensitive to individual data points or model assumptions. For example, while choice of the natural mortality rate may have large effects for the estimation of certain quantities such as stock abundance and exploitation rate, the impact on the estimate of a quantity directly utilized by managers such as the total allowable catch may be quite small (ICES 1986). In fact it is generally not possible to draw conclusions about the uncertainty in final model outputs simply by examining the variability in the input data (e.g., a 20% coefficient of variation (CV) in a survey index used in an assessment does not mean the estimates of stock abundance will have a similar CV).

Finally, scientists and managers need to be aware that not all assessments are created equal. Quantitative evaluation of the uncertainty in the scientific advice allows advice from different assessments to be compared. For example, standard advice resulting from an assessment produced by (mainly) government scientists in a working group or plan-development team can be compared with alternative assessments presented by academic or consultant scientists working with one of the fishery interest groups.

In the following sections, basic terminology useful for describing uncertainty is given, examples of advice incorporating uncertainty are described, and a general simulation framework is presented as a tool for risk assessment.

Terminology

In 1992, the U.S. National Marine Fisheries Service formed an ad hoc Risk Assessment Working Group to help develop approaches to risk assessment. The group found the following terminology useful in discussion. *Risk analysis* is the evaluation of benefit streams under uncertainty produced in a *risk assessment* using a specified loss or utility function. *Risk* is the expected loss of benefits from the resource. *Probability profiles* express the cumulative probability of different outcomes from an assessment or a management scenario produced in an *uncertainty analysis* of the various sources of error described below. These definitions accord with those used in decision theory (e.g., see Kim 1992). Note that the definition of risk requires a specification of the loss or utility function giving the relative value of different possible outcomes. In other words, it is necessary to determine the consequence of obtaining a given outcome before the risk associated with an action which may result in that outcome is evaluated. This definition of risk can be used more generally for a wider range of loss functions than the simple loss function that has been used in fisheries when calculating "the probability of something bad happening" (e.g., Francis 1992; Restrepo et al. 1992).

At least five types of uncertainty can be distinguished: (1) measurement error is the error in the observed quantities such as the catch or average size at age; (2) process error is the underlying stochasticity in the population dynamics such as random variability in recruitment; (3) model error is the misspecification of model parameter values (e.g., the natural mortality rate) or structure; (4) estimation error can result from any of the above uncertainties and is the inaccuracy and imprecision in the estimated model parameters such as stock abundance or fishing mortality rate; and (5) implementation error results from variability in the resulting implementation of a management policy, i.e., inability to achieve a target harvest strategy exactly.

Each source of uncertainty is present in any fish stock assessment, although they are not always explored in each analysis. In general the first two have been the most widely explored (Shepherd 1991; Smith et al. 1993).

Examples of the Analysis of Uncertainty

Uncertainty analyses have become a routine component of the assessment advice for many stocks assessed by NMFS scientists in all regions of the United States. This is not to say that each assessment includes such an analysis, but that the methodology has been developed and applied for some important stocks. Here, a few examples indicate the types of analyses. This list is in no way intended to be exhaustive.

Northeastern United States

In the northeastern United States, biannual stock assessments workshops are held to peer review advice on high-priority stocks such as groundfish (Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), summer flounder (*Paralichthys dentatus*), yellowtail flounder (*Pleuronectes ferrugineus* (previously *Limanda ferruginea*)), sea scallop (*Placopecten magellanicus*), and American lobster (*Homarus americanus*) (NEFSC 1993). For analytical assessments on these stocks the error in the estimates of current status is obtained by bootstrapping (Efron 1982) the final assessment run to produce frequency distributions of stock abundance and fishing mortality rate estimates for the most recent year. The resampled quantities are the residuals from the fitted assessment and the observed indices of relative abundance (Conser 1994). These estimates are presented in the report to managers in the form of probability profiles which express the chance that the stock abundance (fishing mortality rate) is greater than (less than) a quantity given on the abscissa of the graph. The advisory statements are then of the form "there is an *X*% probability that the fishing mortality rate exceeded *Y*, the level of fishing mortality corresponding to the definition of overfishing in the Fishery Management Plan" (NEFSC 1993). In addition, for some of the stocks in the northeast, stochastic projections including process error in the form of recruitment variability are presented as part of the advice (NEFSC 1994). Then,

a distribution of projected stock abundance in future years is obtained for each of a set of management options. Combining the estimation error for the current status and the process error for the future trajectories enables managers to evaluate trade-offs between management strategies. For development of the most recent amendment to the groundfish management plan, this evaluation included analysis of the economic trade-offs between different policy options (Overholtz et al. 1993).

Southeastern United States and ICCAT

In the southeast United States, relatively few of the stocks under federal management can be assessed analytically with age-structured assessments. However, for some of the major stocks, such as king mackerel (*Scomberomorus cavalla*) and Spanish mackerel (*Scomberomorus maculatus*), an extensive uncertainty analysis has been conducted using the approach described by Restrepo et al. (1992) and Powers and Restrepo (1993), which employs Monte Carlo techniques to account for measurement and process errors in the assessment. Members of a scientific stock assessment panel examine all the inputs used for sequential population analysis (ADAPT; Gavaris 1988; Powers and Restrepo 1992) to make decisions about their uncertainty. In some cases these decisions are straightforward and based on statistical considerations, e.g., annual relative abundance estimates may be considered to be lognormally distributed with variances estimated in a General Linear Model (McCullagh and Nelder 1986). In other cases, decisions are based on educated guesses such as the likely range of plausible values for the natural mortality rate (which is not estimated by the assessment model). Once the input uncertainties are agreed upon by consensus, the assessment is repeated a large number of times (e.g., 1000), each time drawing inputs randomly from the specified distributions. Short-term stochastic projections are subsequently made for different management options while maintaining consistency in the random input values. For instance, the 12th sequential population analysis and the 12th projection are associated with the same value of natural mortality. The assessment or projection outputs of interest are then summarized as frequency distributions or probability profiles which form the basis of scientific advice (Powers 1993). The Monte Carlo approach is thus used to translate the collective uncertainty about input data and assumptions into uncertainty in the scientific advice for management.

For the past 3 yr, the Gulf and South Atlantic Fishery Management Councils have made use of probability profiles that summarize the scientists' uncertainty about the key questions that need to be addressed under their Fishery Management Plans designed to rebuild stocks of king and Spanish mackerels: What is the probability that the current F exceeds the overfishing definition and by how much? For a given total allowable catch (TAC) next year or the year after, what is the probability that overfishing will take place? Given this information, the Management Councils agree on a TAC that will not change much from previous years (so as not to cause disruptions to the industry) while maintaining the probability of overfishing at a low level.

Scientists from the southeastern United States are also involved in assessments of swordfish, billfishes, and tunas conducted by ICCAT, the International Commission for the Conservation of Atlantic Tunas. The methods used to express uncertainty in the analyses are either Monte Carlo techniques, as described above, or bootstrapping (Restrepo et al. 1992). The evaluation of uncertainty focuses primarily on relative quantities such as (a) current stock status relative to some time in the past, (b) current exploitation rate relative to biological reference points, and (c) projected stock status at some time in the future under different management scenarios, relative to the present. The assessments of these stocks are often highly controversial and political with a number of nations and interest groups involved. The analyses are intended to allay concerns over the scientific advice by confronting uncertainty directly. In addition to estimates of the measurement error in the current status and stochastic projections of both measurement and process errors, the assessment advice includes sensitivity analysis of model assumptions and estimates of the uncertainty in biological reference points (ICCAT 1993).

Pacific Coast

Many of the important Pacific coast stocks are assessed using the Stock Synthesis method (Methot 1990). Examples include major rockfish stocks such as bocaccio (*Sebastes paucispinis*) and widow rockfish (*Sebastes entomelas*), Pacific hake (*Merluccius productus*), and northern anchovy (*Engraulis mordax*) (NOAA 1991). These assessments contain sensitivity analysis of model errors along with profiles of the objective function (from the maximum likelihood estimation procedure) for key parameter estimates to depict uncertainty in the estimates of stock status (Pacific Fishery Management Council 1992).

For some fisheries, simulation studies of uncertainty have been conducted. Analysis of alternative harvest policies of the multispecies rockfish fishery was described by Hightower (1990). Bence et al. (1993) described the relation between survey selectivity and assessment accuracy and precision. The northern anchovy Fishery Management Plan contains an analysis of alternative harvest policies under uncertainty as part of the development of a management strategy (Pacific Fishery Management Council 1990). Stochastic simulations of the Pacific hake resource have been used to compare alternative management strategies by Dorn et al. (1991). Stochastic simulations were also used to examine some management options for Klamath River chinook salmon (*Oncorhynchus tshawytscha*) (R. Kope, NMFS Tiburon Lab, 3150 Paradise Drive, Tiburon, Calif., personal communication). Kope (1992) has examined the more general question of harvesting mixed stocks of natural and hatchery salmon under uncertainty via a dynamic programming approach.

These studies project the effects of process and estimation error forward in the evaluation of strategies, including the assessment of risk in the cases of salmon and anchovy. These types of analyses are not standard components of the management advice as yet, but are increasingly used for the development of west coast Fishery Management Plans.

Alaska

In Alaska, analyses of uncertainty in the stock assessment advice have largely consisted of sensitivity analyses of model error. However, risk analyses considering uncertainty due to estimation and/or process error have been done for a several stocks. Thompson (1989) developed harvest recommendations for eastern Bering Sea Pacific cod (*Gadus macrocephalus*) from a Bayesian risk analysis (see Thompson

1992 for a description of the methodology). A bioeconomic stochastic simulation model of the Gulf of Alaska walleye pollock (*Theragra chalcogramma*) resource has been developed by Megrey et al. (1993). Comparisons of the economic performance and the conservation risk to the resource due to low stock size were made for a range of harvest rate options. For Atka mackerel (*Pleurogrammus monopterygius*), Lowe and Thompson (1993) examined policy options for expansion of the fishery by considering trade-offs between expected yield and the stability of yield as measures of utility. They used both linear and logarithmic utility functions, the latter to evaluate risk averse strategies. Alternative policies for the Pacific ocean perch (*Sebastes alutus*) fishery in the Gulf of Alaska have been evaluated using stochastic simulations incorporating the assessment of risk in a decision table framework (Ianelli and Heifetz 1994). For sablefish (*Anoplopoma fimbria*), Sigler and Fujioka (1993) examined five alternative management scenarios incorporating measurement and process error in the projections. Again, although these types of analyses are not yet standard parts of management advice, they are being used increasingly by managers in the development of policy.

Towards a Risk Assessment Methodology

From the work that has been done to date, there are four clear steps in the preparation of uncertainty analyses and risk assessments: (1) analysis of estimation error, (2) sensitivity to model errors, (3) stochastic projections, and (4) risk analysis.

A first step should be estimation of the uncertainty in the estimate of current stock status (abundance and fishing mortality rate) and biological reference points. This type of analysis typically focuses on measurement and estimation errors and results in probability profiles for estimated model parameters. The analysis may be done by Monte Carlo simulation, analytically, or via a bootstrap approach, but the last may be easiest because it requires the fewest explicit assumptions. Note that the uncertainty that is required pertains to quantities that may not be directly estimated in the assessment itself. For example, it is common to estimate the stock abundance at age or size, but the quantity of interest for management advice is more often the total fishable biomass. For such aggregate parameters, analytical estimates of uncertainty may be intractable except in cases where the delta method (Seber 1982) can be applied.

In the second step, model error may be analyzed using simple sensitivity analysis (Majkowski 1982). For example, impact on the final advice of assumptions concerning the rate of natural mortality or different forms of the relationship between catch per unit effort and abundance can be explored through alternative assessment runs using different models. A full sensitivity analysis may use a Monte Carlo method to explore a range of model forms or parameter values. Note, however, that sensitivity analysis is not needed to explore the measurement error in specific data points unless there is clear evidence that one point is likely to be more imprecise or inaccurate than the others. Although it is common practice to examine the effect of subjectively excluding one data point or another (e.g., ICCAT 1993), uncertainty due to measurement error is better addressed by bootstrapping simulations in step one except if there is objective information concerning a given datum. Examining sensitivity to individual data points in isolation may give them too much emphasis in the overall advice.

The third step is stochastic projections including the estimation error in current status and the process error in the projected period. Short-term projections (i.e., for years in which advance estimates of recruitment are available) focus primarily on estimation error. Long-term projections focus on process and possibly implemention errors (e.g., Rosenberg and Brault 1993). Process error will result mainly from random variability in recruitment, so some form of a stochastic relationship between stock and recruitment is needed. This should be based on the historical data, although it need not take the form of a parametric stock and recruitment curve (e.g., Ianelli and Heifetz 1994). For any projections, a range of possible management strategies will need to be explored. The results of stochastic projections are probability profiles of the outcome for different key management quantities such as stock abundance, yield, or economic variables such as producer and consumer surplus.

While simple, long-term stochastic projections incorporate process errors through a stochastic stock and recruitment relationship, it is important to realize that measurement and estimation errors will remain important sources of uncertainty for evaluating the future of the resource (Bergh and Butterworth 1987; Punt 1991). More complex projections including estimation error may involve simulating the assessment process itself forward in time. A system to do this, in which management strategies can be compared by projecting forward in time from the current status of the resource, generating new observations on the fishery with measurement error each projection year, and reassessing the stock, was described by Restrepo et al. (1992), Rosenberg and Restrepo (1993), and Restrepo and Rosenberg (1994). These simulations can also be used to evaluate the benefit of reducing measurement errors through additional research (Powers and Restrepo 1993).

The final step is to calculate measures of risk as expected loss over time using plausible loss or utility functions, preferably provided by resource managers. This is undoubtedly a difficult task for two reasons. First, managers or management bodies do not usually state their objectives in a form that can be used to construct utility or loss functions. Moreover, individual decision makers in a management body usually have multiple objectives that differ from each other's and whose relative importance may change from year to year depending on a variety of socioeconomic and political factors. Second, advances in population dynamics and stock assessment tools and advances in the economic theory of fishing have been largely independent for several decades. As a result, managers are usually presented two separate sets of information from which they contemplate "risks" to the industry and "risks" to the population. These two types of information are rarely presented to managers together in a stock assessment report, with the exception of projected short-term catches which are used as a proxy for revenues.

We believe that these problems can be solved. While individual decision makers are not likely to define utility functions in the future, requirements for management plans are limiting the range of decisions they can make. An example of this in the United States are the "602 Guidelines" (Department of Commerce 1989) which require all fishery management plans to define recruitment overfishing and recovery plans for overfished stocks. The 602 Guidelines do not

define loss functions per se, but facilitate their construction. As to the second problem, all the necessary computational and theoretical tools are available to combine economic and biological considerations in the evaluation of management alternatives. There are already a number of excellent bioeconomic policy models as noted above (e.g., Megrey et al. 1993). Much of the discussion of policy options for rebuilding overfished stocks centers on the trade-off between short-term losses versus long-term gains. While past assessment advice has typically restricted projections to the short term, management strategy evaluation requires longer-term prognoses for the stock. The long-term projections must include some form of a stock and recruitment relationship as well as the inclusion of as much detail as possible concerning the economic performance of the fishery.

Hilborn et al. (1993) proposed a two-step process to deal with uncertainty and risk explicitly in stock assessment advice. In the first step, a stock assessment group determines possible "states" of the stock and evaluates the impacts of alternative management actions for each state. In the second step, decision makers examine the losses and benefits (to the stock and the industry) for each "state" that would be associated with each management alternative and then reach a decision. This process is compatible with the ideas in our presentation and with current efforts to confront uncertainty in stock assessments the United States. However, we disagree with Hilborn et al.'s (1993) suggestion that scientists should not attempt to make "best" estimates in deciding about possible "states" of the stock. All computations of stock status, biological reference points, and effects of alternative management actions are conditional on the data, models, and assumptions used. Trained scientists and economists knowledgeable about a particular stock ought to be able to judge which assumptions and data are "better" than others and make a "best" recommendation even if it involves additional uncertainty in the form of an "educated guess". Many stock assessments are conducted with different types of models and data (e.g., nonequilibrium production models and sequential population analyses), and their estimation of the stock's "state" may or may not differ. Given scientists' knowledge of the species, the data, and simulation experiments, it should be possible to pick one as the preferable solution. In cases where not only the estimation of stock status differs, but the evaluation of the impact of alternative management decisions also differs, the robustness of the entire management procedure to the different models can be investigated via simulation (see Punt 1991).

Acknowledgements

This work has benefitted from discussions of the National Marine Fisheries Service's ad hoc Risk Assessment Working Group and the International Council for the Exploration of the Seas' Stock Assessment Methods and Long-term Management Measures Working Groups. We also thank G.G. Thompson and R.I.C.C. Francis for their helpful comments. Partial support was provided through the Cooperative Unit of Fisheries Education and Research by National Oceanic and Atmospheric Administration Cooperative Agreement No. NA37RJ0200.

References

BENCE, J.R., A. GORDOA, AND J.E. HIGHTOWER. 1993. Influence of age-selective surveys on the reliability of stock synthesis assessments. Can. J. Fish. Aquat. Sci. 50: 827–840.

BERGH, M.O., AND D.S. BUTTERWORTH. 1987. Towards rational harvesting of the South African anchovy considering survey imprecision and recruitment variability. S. Afr. J. Mar. Sci. 5: 937–951.

CONSER, R.J. 1994. Stock assessment methods designed to support fishery management decisions in data-limited environments: development and application. Ph.D. dissertation, University of Washington, Seattle, Wash.

DEPARTMENT OF COMMERCE. 1989. 50 CFR Part 602: guidelines for fishery management plans. U.S. Fed. Regist. 54(140): 30711–30880.

DORN, M.W., R.D. METHOT, E.P. NUNNALLEE, AND M.E. WILKINS. 1991. Status of the coastal Pacific whiting resource in 1990. NOAA Tech. Memo. NMFS F/NWC-204.

EFRON, B. 1982. The jacknife, the bootstrap and other resampling plans. Society for Industrial and Applied Mathematics, Philadelphia, Pa. 92 p.

FRANCIS, R.I.C.C. 1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy *Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. Can. J. Fish. Aquat. Sci. 49: 922–930.

GAVARIS, S. 1988. An adaptive framework for the estimation of population size. CAFSAC (Can. Atl. Fish. Sci. Adv. Comm.) Res. Doc. 88/29.

GETZ, W.M., R.C. FRANCIS, AND G.L. SWARTZMAN. 1987. On managing variable marine fisheries. Can. J. Fish. Aquat. Sci. 44: 1370–1375.

HIGHTOWER, J.E. 1990. Multispecies harvesting policies for Washington–Oregon–California rockfish trawl fisheries. Fish. Bull. U.S. 88: 645–656.

HILBORN, R., E.K. PIKITCH, AND R.C. FRANCIS. 1993. Current trends in including risk and uncertainty in stock assessment and harvest decisions. Can. J. Fish. Aquat. Sci. 50: 874–880.

IANELLI, J.N. AND J. HEIFETZ. 1994. A decision analysis of alternative harvest policies for the Gulf of Alaska Pacific ocean perch fishery. National Marine Fisheries Service Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, Wash. 26 p.

ICCAT. 1993. Report of the Standing Committee on Research and Statistics 1993. International Commission of the Conservation of Atlantic Tunas, Madrid, Spain.

ICES. 1986. Report of the Working Group on Methods of Fish Stock Assessment. ICES C.M. 1986/Assess: 10.

ICES. 1993. Report of the Working Group on Methods of Fish Stock Assessment. ICES Doc. C.M. 1993/Assess: 7.

KIM, S.H. 1992. Statistics and decisions. An introduction to foundations. Van Nostrand Reinhold, New York, N.Y.

KOPE, R.G. 1992. Optimal harvest rates for mixed stocks of natural and hatchery fish. Can. J. Fish. Aquat. Sci. 49: 931–938.

LOWE, S.A., AND G.G. THOMPSON. 1993. Accounting for uncertainty in the development of exploitation strategies for the Atka mackerel resource of the Aleutian Islands. Alaska Sea Grant College Program AK-93-02. University of Alaska, Anchorage, Alaska.

LUDWIG, D., R. HILBORN, AND C. WALTERS. 1993. Uncertainty, resource exploitation and conservation: lessons from history. Science (Wash., D.C.) 260: 17.

MAJKOWSKI, J. 1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. ICLARM Conf. Proc. 9: 149–165.

MCCULLAGH, P., AND J.A. NELDER. 1986. Generalized linear models. Chapman and Hall, London.

MEGREY, B.A., A.B. HOLLOWED, AND R.T. BALDWIN. 1993. Sensitivity of patimum harvest strategy estimates to alternative definitions of risk. ICES C.M. 1993/D:38. Copenhagen, Denmark.

METHOT, R.D. 1990. Synthetic estimates of historical abundance and mortality for northern anchovy. Am. Fish. Soc. Symp. 6: 66–82.

NEFSC. 1993. Report of the 16th Northeast Regional Stock Assessment Workshop. Northeast Fish. Sci. Center Ref. Doc. 93-18: 118 p.

NEFSC. 1994. Report of the 17th Northeast Regional Stock Assessment Workshop. Northeast Fish. Sci. Center Ref. Doc. 94-06: 124 p.

NOAA. 1991. Status of living marine resources off the Pacific Coast of the United States as assessed in 1991. NOAA Tech. Memo. NMFS-F/NWC-210: 69 p.

OVERHOLTZ, W.J., S.F. EDWARDS, AND J.K.T. BRODZIAK. 1993. Strategies for rebuilding and harvesting New England groundfish resources. Alaska Sea Grant College Program AK-93-02. University of Alaska, Anchorage, Alaska.

PACIFIC FISHERY MANAGEMENT COUNCIL. 1990. Sixth amendment to the northern anchovy fishery management plan. Pacific Fishery Management Council, Portland, Oreg.

PACIFIC FISHERY MANAGEMENT COUNCIL. 1992. Appendices to the status of the Pacific Coast groundfish fishery through 1992 and recommended acceptable biological catches for 1993. Pacific Fishery Management Council, Portland, Oreg. 335 p.

POWERS, J.E., AND V.R. RESTREPO. 1992. Additional options for age-

sequenced analysis. ICCAT (Int. Comm. Conserv. Atl. Tunas) Collect. Vol. Sci. Pap. 39: 540–553.

POWERS, J.E., AND V.R. RESTREPO. 1993. Evaluation of stock assessment research for Gulf of Mexico king mackerel: benefits and costs to management. N. Am. J. Fish. Manage. 13: 15–26.

PUNT, A.E. 1991. Management procedures for the Cape hake and baleen whale resources. Benguela Ecol. Programme Rep. No. 23.

RESTREPO, V.R., J.M. HOENIG, J.E. POWERS, J.W. BAIRD, AND S.C. TURNER. 1992. A simple simulation approach to risk and cost analysis, with applications to swordfish and cod fisheries. Fish. Bull. U.S. 90: 736–748.

RESTREPO, V.R., AND A.A. ROSENBERG. 1994. Evaluating the performance of harvest control laws under uncertainty via simulation. ICES Longterm Management Measures Working Group Working Doc. No. 18, January 1994, Miami, Fla.

ROSENBERG, A.A., AND S. BRAULT. 1993. Choosing a management strategy for stock rebuilding when control is uncertain, p. 243–252. *In* S.J. Smith, J.J. Hunt, and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish Aquat. Sci. 120.

ROSENBERG, A.A., AND V.R. RESTREPO. 1993. The eloquent shrug: expressing uncertainty and risk in stock assessments. ICES 1993 C.M. D:12, Sess.: P.

SEBER, G.A.F. 1982. The estimation of animal abundance and related parameters. 2nd ed. Charles Griffin and Co., London.

SHEPHERD, J.G. 1991. Special session on management under uncertainties. NAFO Sci. Counc. Stud. 16: 7–12.

SIGLER, M.F., AND J.T. FUJIOKA. 1993. Harvest policies for sablefish in the Gulf of Alaska. Alaska Sea Grant College Program AK-93-02.

SMITH, S.J., J.J. HUNT, AND D. RIVARD. 1993. Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120: 442 p.

THOMPSON, G.G. 1989. Pacific cod, p. 46–59. *In* Plan Team of the Groundfish Fisheries of the Bering Sea and Aleutian Islands [ed.] Stock assessment and fishery evaluation document for groundfish fisheries in the Bering Sea/Aleutian Islands region as projected for 1990. North Pacific Fishery Management Council, P.O. Box 103136, Anchorage, Alaska.

THOMPSON, G.G. 1992. A Bayesian approach to management advice when stock–recruitment parameters are uncertain. Fish. Bull. U.S. 90: 561–573.

Introduction to Experimental Lakes and Natural Processes: 25 Years of Observing Natural Ecosystems at the Experimental Lakes Area

R.E. Hecky, P. Campbell, and D.M. Rosenberg

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

The Experimental Lakes Area (ELA) in northwestern Ontario was created to allow whole-lake manipulations to be added to the suite of research methods used to understand how pollutants can affect lake ecosystems (Johnson and Vallentyne 1971). The more than 550 publications attributable to the ELA are dominated by papers explaining and interpreting those whole-lake experiments. Most of those papers refer to observations in natural systems as the standard against which an experimental effect is assessed. The ELA was not created to produce long-term and comparative studies of lakes and their watershed inputs, but it has, of necessity, done so in the course of its 25-yr history of experimentation.

Experimental Lakes Area researchers have not been the only source of perturbations. Significant natural impacts have been imposed on the ELA by windstorms and forest fires, which nearly devastated the facility in 1974 and 1980 (Bayley et al. 1992a, 1992b), and by climatic variation, in particular the warm, dry 1980s (Schindler et al. 1990). Ongoing ELA programs that were using unperturbed systems as references enabled monitoring and interpretation of the effects of these natural disturbances long before the Long-Term Ecological Research (LTER) program (Callahan 1984) was funded. The value of the ELA long-term records on natural systems has now been recognized by the recent Department of Environment designation of the ELA as an Ecosystem Science Centre. The ELA program itself has also recognized the importance of long-term records by creating a central electronic database to archive 25 yr of information and make it accessible to the research community.

The following seven papers are concerned with natural variability; they are indicative of how studies on natural systems have contributed to the success of the ELA program. These papers make up the second of three groups of contributions that celebrate the 25th anniversary of the ELA. The first set appeared in the October 1994 issue of the *Canadian Journal of Fisheries and Aquatic Sciences* (Vol. 51). The third set, dealing with contaminants, will be published in 1995.

Variability in natural aquatic systems is observed over a range of temporal and spatial scales (e.g., Resh and Rosenberg 1989). Daily oscillations in radiant energy create constant physiological and behavioural flux in biological populations. In addition, seasonal changes in insolation impose temperature and stratification cycles on lakes that further shape lake community structures and dynamics. Aquatic organisms from bacteria to fish respond to these energy fluxes at different time scales, based on their own life-history characteristics. Periodic alterations in energy fluxes and population responses can seem predictable in a lake studied over a few years, but longer term studies often reveal complex adjustments in internal processes. Long-term studies can also capture unusual and catastrophic events that can disrupt the illusion of regularity and predictability. Over the very long term, such events probably will not seem that unusual (e.g., the vegetative composition of boreal forests is dictated by an infrequent and irregular cycle of fire).

Spatially, observations made in a single lake may or may not be broadly applicable across a region. Each lake has an unique set of morphometric and watershed characteristics that are overlain on broad regional variations in hydrology, vegetation, soils, and surficial geology. Limnologists, most notably D.S. Rawson in Canada, have long recognized this complex interplay of climate, morphometry, and geology in determining the character of lakes and their fisheries, but systematic research on this complexity is difficult to do. Studies of the landscape ecology of lakes have an important future, and will surely accelerate as methods for remote observation and geographic information systems are wedded with more traditional watershed and lake studies. Recent ELA contributions to this evolving field of research are multiyear studies of the effect of spatial scale on lake processes (Fee and Hecky 1992; Fee et al. 1992), and the importance of hydraulic flushing, morphometry, and watershed characteristics in defining some critical properties of lakes (Campbell 1993; McCullough and Campbell 1993).

The papers in this series can be arbitrarily divided into those that primarily treat spatial aspects of variability (Turner et al. 1994; Fee et al. 1994; Guildford et al. 1994) and those that primarily deal with temporal variability (Beaty 1994; Schindler et al. 1994; Campbell 1994; Findlay et al. 1994). However, in reality, it is difficult to separate spatial and temporal variability. All the papers involve many years of data and all, except for Beaty (1994), refer to more than one system.

Experimental disruptions often elucidate processes that cannot be easily appreciated or studied in the natural state, which is why whole-system experiments almost always provide some unexpected results; such surprises lead to new insights and understanding. Turner et al. (1994) began with an anomolous result from a whole-lake nutrient enrichment experiment in which phytoplankton productivity was dramatically increased whereas phytobenthic productivity was unchanged. Using a combination of comparative and experimental research, Turner et al. (1994) conclude that there is carbon limitation of benthic algal photosynthesis in natural, soft-water lakes. Fee et al. (1994) use a classical comparative approach to demonstrate that photosynthesis in small lakes is more dependent on external nutrient loading than in large lakes, and conclude that this difference arises from more efficient nutrient regeneration in large systems. Guildford et al. (1994) demonstrate directly that small-lake planktonic communities are more nutrient deficient than similar communities in large systems, and also conclude

that nutrient cycling in small systems is less efficient than in large systems. The last two contributions address a question originally posed by Johnson and Vallentyne (1971): Can the results and interpretation of experiments in small lakes be applied to much larger systems? The answer is a qualified yes. For example, phytoplankton communities in all the lakes in the Northwest Ontario Lake Size Series (NOLSS) set, from small ELA lakes to Lake Superior, are phosphorus deficient and share a common chlorophyll–phosphorus relationship (Guildford et al. 1994). However, it is necessary to recognize appropriate physical scaling factors to predict other aspects of phytoplankton ecology such as algal growth rates. In fact, spatial scaling factors are required to apply results from small, model systems to larger systems, whether they are lakes or airplanes. Of course, this successful application requires that the model systems, ELA lakes, include all the essential processes and functional components of the large systems. Studies involving subdivision of a lake system into subsystems such as limnocorrals and bottles can yield insights into processes, but data from such studies cannot be directly applied to larger systems because the subsystems do not include all the properties of the larger systems (Hecky and Kilham 1988).

The temporal variability of processes and structure in lakes makes it difficult to take meaningful measurements (Beaty 1994; Schindler et al. 1994), fully define long-term cycles (Campbell 1994), and identify sources of variance; old disturbances can generate persistent effects (Findlay et al. 1994). Flow and resultant sediment and bedload transport are highly variable in small streams. Stream measurements increase in difficulty when questions are asked about variability in these processes at annual time scales or in response to catastrophic events such as windstorms and forest fires. Beaty (1994) shows that the answer to such questions requires a rigorous method and nearly continuous sampling. Similarly, short-term variability in phytoplankton (e.g., doubling rates from hours to days) is always a concern to long-term estimates of various processes because measurement frequencies differ at different temporal scales. However, the problem of estimating photosynthesis is manageable in ELA lakes (Schindler et al. 1994); a few measurements in critical seasons are more important to annual estimates of photosynthesis than many measurements at daily time intervals. Sometimes, though, detail is necessary. For example, Campbell (1994) uses high-resolution vertical chemical profiles to determine the seasonal cycling of phosphorus in unmanipulated ELA lakes. The spatial detail is necessary because small, deep lakes in the ELA exhibit extreme variance in nutrient concentrations over short distances as functions of sharp thermal stratification and metalimnetic algal blooms. Campbell (1994) also concludes that sediment regeneration is a significant source of nutrients to sustain algal production through the open-water season.

Findlay et al. (1994) describe changes that occurred in the pelagic plankton after introduction of a top predator to a cyprinid-dominated lake. They conclude that such a food-chain perturbation led to redistribution of phosphorus among the biotic components of the lake, but phytoplankton growth remained phosphorus limited. The succession of biological events that occurred for several years after the introduction of the piscivore provides a warning against short-term interpretation of experiments on natural ecosystems; long-term ecological adjustments may overcome some of the most prominent short-term effects. The study is also extremely instructive about the responses of different parts of the lacustrine biocoenosis. For example, nutrient redistributions among biota probably occur naturally with density-dependent or density-independent population fluctuations of top predators in a lake. As with Turner et al. (1994), the results of the Findlay et al. (1994) experiment lead to insights about obscure but critical processes.

Studies of natural systems have not only been essential to the success of whole-lake experiments at the ELA, but such studies have made their own unique and important contributions to ecosystem science. Long-term studies and landscape analysis are increasingly accepted approaches to ecosystem issues and questions of global change. The study of natural systems at the ELA now has its own raison d'être.

References

BAYLEY, S.E., D.W. SCHINDLER, K.G. BEATY, B.R. PARKER, AND M.P. STAINTON. 1992a. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorous. Can. J. Fish. Aquat. Sci. 49: 584–596.

BAYLEY, S.E., D.W. SCHINDLER, B.R. PARKER, M.P. STAINTON, AND K.G. BEATY. 1992b. Effects of forest fire and drought on acidity of a base-poor boreal forest stream: similarities between climatic warming and acidic precipitation. Biogeochemistry 17: 191–204.

BEATY, K.G. 1994. Sediment transport in a small stream following two successive forest fires. Can. J. Fish. Aquat. Sci. 51: 2723–2733.

CALLAHAN, J.T. 1984. Long-term ecological research. BioScience 34: 363–367.

CAMPBELL, P. 1993. Lake variation and climate change study: ELA lakes, 1986–1990. I. Study rationale and lake selection criteria. Can. Tech. Rep. Fish. Aquat. Sci. 1897: 7 p.

CAMPBELL, P. 1994. Phosphorus budgets and stoichiometry during the open-water season in two unmanipulated lakes in the Experimental Lakes Area, northwestern Ontario. Can. J. Fish. Aquat. Sci. 51: 2739–2755.

FEE, E.J., AND R.E. HECKY. 1992. Introduction to the Northwest Ontario Lake Size Series (NOLSS). Can. J. Fish. Aquat. Sci. 49: 2434–2444.

FEE, E.J., R.E. HECKY, G.W. REGEHR, L.L. HENDZEL, AND P. WILKINSON. 1994. Effects of lake size on nutrient availability in the mixed layer during summer stratification. Can. J. Fish. Aquat. Sci. 51: 2756–2768.

FEE, E.J., J.A. SHEARER, E.R. DEBRUYN, AND E.U. SCHINDLER. 1992. Effects of lake size on phytoplankton photosynthesis. Can. J. Fish. Aquat. Sci. 49: 2445–2459.

FINDLAY, D.L., S.E.M. KASIAN, L.L. HENDZEL, G.W. REGEHR, E.U. SCHINDLER, AND J.A. SHEARER. 1994. Biomanipulation of Lake 221 in the Experimental Lakes Area (ELA): effects on phytoplankton and nutrients. Can. J. Fish. Aquat. Sci. 51: 2794–2807.

GUILDFORD, S.J., L.L. HENDZEL, H.J. KLING, E.J. FEE, G.G.C. ROBINSON, R.E. HECKY, AND S.E.M. KASIAN. 1994. Effects of lake size on phytoplankton nutrient status. Can. J. Fish. Aquat. Sci. 51: 2769–2783.

HECKY, R.E., AND P. KILHAM. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. Limnol. Oceanogr. 33: 796–822.

JOHNSON, W.E., AND J.R. VALLENTYNE. 1971. Rationale, background, and development of experimental lake studies in northwestern Ontario. J. Fish. Res. Board Can. 28: 123–128.

MCCULLOUGH, G.K., AND P. CAMPBELL. 1993. Lake variation and climate change study: ELA lakes, 1986–1990. II. Watershed geography and lake morphology. Can. Tech. Rep. Fish. Aquat. Sci. 1898: 29 p.

RESH, V.H., AND D.M. ROSENBERG. 1989. Spatial-temporal variability and the study of aquatic insects. Can. Entomol. 121: 941–963.

SCHINDLER, D.W., K.G. BEATY, E.J. FEE, D.R. CRUIKSHANK, E.R. DEBRUYN, D.L. FINDLAY, G.A. LINSEY, J.A. SHEARER, M.P. STAINTON, AND M.A. TURNER. 1990. Effects of climatic warming on lakes of the central boreal forest. Science (Wash., DC) 250: 967–970.

SCHINDLER, E.U., E.R. DEBRUYN, E.J. FEE, AND J.A. SHEARER. 1994. Sensitivity of estimates of seasonal phytoplankton photosynthesis to sampling frequency. Can. J. Fish. Aquat. Sci. 51: 2734–2738.

TURNER, M.A., E.T. HOWELL, G.G.C. ROBINSON, P. CAMPBELL, R.E. HECKY, AND E.U. SCHINDLER. 1994. Roles of nutrients in controlling growth of epilithon in oligotrophic lakes of low alkalinity. Can. J. Fish. Aquat. Sci. 51: 2784–2793.

Sediment Transport in a Small Stream following Two Successive Forest Fires[1]

K.G. Beaty

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Beaty, K.G. 1994. Sediment transport in a small stream following two successive forest fires. Can. J. Fish. Aquat. Sci. 51: 2723–2733.

The transport of stream bedload sediment was monitored continuously in a small stream from 1975 to 1982 following forest fires in 1974 and 1980. The stream is located in the east subcatchment (170 ha) of Lake 239 in the Experimental Lakes Area, northwestern Ontario. Precipitation, stream discharge, bedload transport, and concentration of suspended materials were measured quantitatively and organic debris was observed and collected. Bedload transport increased 20-fold following the first fire and threefold after the second. Particle sizes tended to increase during the period of study. Bedload data suggest a recovery period of 5–6 yr following the first fire and a shorter one following the second. A mass budget of material load transported in a single year following recovery indicated a dominance of dissolved load (87%), followed by suspended load (10%), and bedload (3%).

Le transport de la charge de fond d'un petit cours d'eau a été étudié de façon continue entre 1975 et 1982 après que des incendies de forêt se soient produits en 1974 et 1980. Le cours d'eau est situé dans la portion est (170 ha) du bassin versant du lac 239 de la région des lacs expérimentaux, dans le nord-ouest de l'Ontario. On a effectué des mesures quantitatives des précipitations, du débit, du transport de la charge de fond et de la concentration des matières en suspension, et observé et recueilli des débris organiques. On a observé un transport de la charge de fond 20 fois plus important après le premier incendie et trois fois plus important après le second. La taille des particules tendait à être de plus en plus élevée avec le temps au cours de la période de l'étude. D'après les données sur la charge de fond, la période de rétablissement aurait été de 5 à 6 ans dans le cas du premier incendie et plus courte après le deuxième incendie. Le bilan massique de la charge de matières transportée au cours d'une année post-rétablissement a montré qu'il y avait dominance de la charge dissoute (87%), suivie de la charge en suspension (10%) et de la charge de fond (3%).

Received October 8, 1993
Accepted July 12, 1994
(J12120)

Reçu le 8 octobre 1993
Accepté le 12 juillet 1994

On June 26, 1974, a severe forest fire burned much of the Experimental Lakes Area (ELA), including the entire eastern subcatchment of Lake 239. This event provided a rare opportunity to study the effects of natural fire on sediment export from a forested watershed. The eastern subcatchment completely reburned 6 yr later, providing an interesting extension to the original data. Water and chemical budgets before the first fire were prepared by Schindler et al. (1976); increased runoff and chemical losses following the fire were documented in Schindler et al. (1980) and Bayley et al. (1992a, 1992b). This study deals primarily with the effect of fire on bedload transport.

Natural wildfire affects runoff and erosion in a forest ecosystem. For example, runoff increased by 60% after burning of the Meander Lake catchment, which is located in an area similar to that of the ELA (Bradbury et al. 1975). Fire results in a loss of vegetation and the organic mat, and a loosening of surface soil and rocks (Hewlett 1982). In the absence of plants to intercept rainfall during storms, there is no protection for mineral soil (Chow 1964; Brown 1972). Exposed coarse soils may allow water to infiltrate readily, whereas fine soils such as clay may absorb moisture, expand, and form a dense waterproof layer that sheds the remainder of the water (Chow 1964).

Soil erosion from deforested watersheds can affect natural resources. For example, increased sedimentation rates may degrade fish spawning sites or insect habitat (Ellis 1936; Tebo 1955; Cordone and Kelly 1961; Peters 1967; Lemly 1982; Fudge and Bodaly 1984; Culp et al. 1986; Rae 1987). However, few studies have focused on the effect of fire on runoff and erosion (Shahlaee et al. 1991), probably partly because of difficulties in quantifying sediment transport.

My objective here is to document the effects of two successive forest fires on the transport of stream bedload sediment in a small Canadian Shield subcatchment. In addition, I describe the importance of bedload sediment relative to total material transport in the study stream.

Study Area

The ELA is located in northwestern Ontario (49°40′N, 93°44′W), ≈56 km southeast of Kenora (Johnson and Vallentyne 1971; Fig. 1A). The geology, soils, and vegetation of the ELA have been described by Brunskill and Schindler (1971) and McCullough and Campbell (1993).

The study site was the eastern subcatchment of Lake 239 (Fig. 1B and 1C), the largest (170 ha) of three well-defined

[1]This paper is one of a series done in honor of the 25th anniversary of the Experimental Lakes Area.

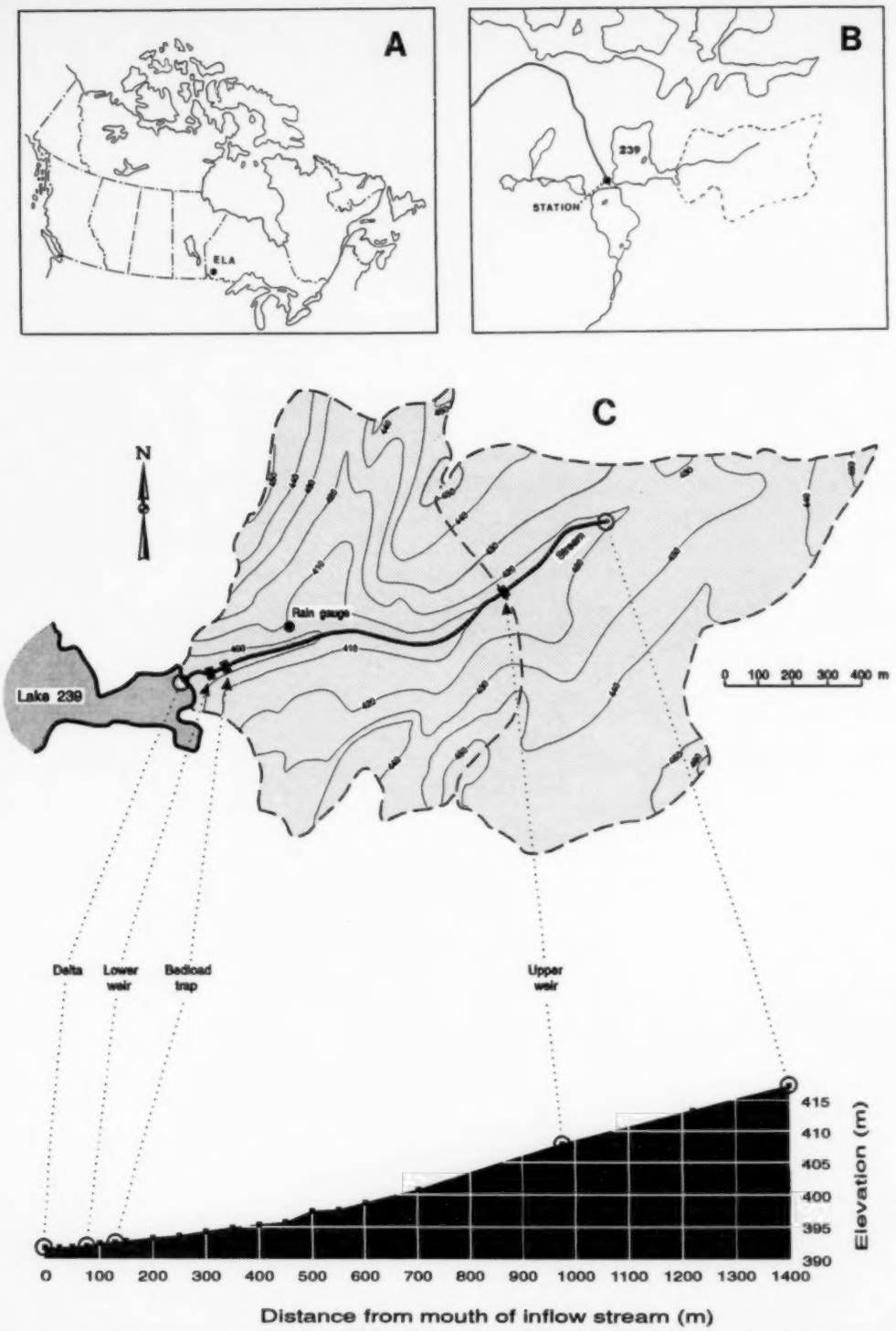


FIG. 1. (A) Location of the Experimental Lakes Area (ELA). (B) Location of Lake 239 and its eastern subcatchment (broken line) within the ELA. The ELA field station is also shown. (C) The eastern subcatchment of Lake 239 and profile of the study stream. Points on the stream profile are elevation survey locations.

terrestrial subcatchments of the lake. The eastern subcatchment lies in an area of glaciated Precambrian terrain with rounded, smooth, and only slightly weathered rock surfaces (Kennedy 1974). The bedrock is predominately pink granodiorite with localized zones of biotite-rich (grey) granodiorite (McCullough and Campbell 1993). Teller (1985) suggested that the area was partially inundated under eastern glacial Lake Agassiz. Quaternary deposits are thin and discontinuous on the hill crests and valley slopes, consisting of granitic, sandy, bouldery till generally <1 m thick. The lowland areas are underlain by up to 16 m of glaciolacustrine sand, silt, and clay. At the lower weir location (Fig. 1C), the flat valley bottom is 130 m wide and is underlain by sandy till. Deltaic deposits of sand at the mouth of the stream are evidence of sediment transport preceeding the first fire. A small, ephemeral stream enters the main stream from the north at ≈400 m from the lake. Flow from this area is poorly defined and enters the main channel through moss and boulders (Bottomley 1974).

The subcatchment is well defined and contained by a high bedrock ridge; groundwater transfer in or out of the subcatchment is unlikely. Maximum relief is 67 m and the average ground slope along the east–west longitudinal axis is 2.7%. The subcatchment is composed of 4% wetland, 6% valley bottom, 10% rock outcrop, and 80% upland (Newbury and Beaty 1977). The main stream channel is ≈1400 m in length (Fig. 1C). From the lake to the upper weir location, the stream channel has a sand bed; the channel is 0.4–1 m wide and, depending on flow condition, is a few centimetres to 0.5 m deep. This reach has a slightly concave, upwards profile and a slope averaging 1.4%. The stream flows over a smooth bedrock sill at ≈1 km from the lake. Above this point, the stream is less well defined; it passes through a wetland area, and has a lower slope than below the bedrock sill.

The climate of ELA is humid continental; mean annual temperature is 2.3°C and average annual precipitation is 673 mm, of which 73% occurs as rain and the remainder as snow (Beaty and Lyng 1989). January is the coldest month; temperatures of −20 to −40°C are common. Midwinter melting is rare and spring snowmelt usually begins by early April and lasts for ≈1 mo. Because of the prolonged melt period and the diurnal freeze–thaw cycle, flows are usually low at this time of the year, unless enhanced by April rainstorms. Forest fires are prevalent in June and July when thunderstorms with intense lightning are most frequent.

Streamflow from the east subcatchment is episodic. During the May to October period, flows are usually sustained by frequent rainstorms. Daily rainfalls exceed 25 mm on only two or three occasions each year. The maximum, mean-daily discharge during the period of study was 0.65 $m^3 \cdot s^{-1}$; the maximum instantaneous peak flow was ≈1 $m^3 \cdot s^{-1}$. Flow exceeds its banks only during major rainstorm events (three or four occasions during this study). In a wet year, the stream may flow continuously; however, in a dry year flow can become intermittent or nonexistent for days to weeks. Freeze-up begins by mid-November, precipitation changes to snow, and streamflow typically diminishes to zero by the end of December.

Before the 1974 fire, the eastern subcatchment was densely forested by commercially valuable, mature stands of jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* Mill.), and isolated groves of white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) (Schindler et al. 1980). Red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and white spruce (*Picea glauca* (Moech) Voss) were less abundant (Bayley et al. 1992a). The oldest trees predated the fire by 100–110 yr (Brunskill and Schindler 1971). The subcatchment contains several small wetland areas formed where sphagnum peat and various shrubs have infilled depressions (McCullough and Campbell 1993).

Virtually all vegetation <2.5 cm in diameter was consumed by the first fire, which started on June 26, 1974. Organic matter in surface soils was mineralized to a depth of several centimetres, and the surface of exposed or thinly covered bedrock was shattered (Schindler et al. 1980). Six years later (June 20, 1980), the eastern subcatchment was again completely burned, and nearly all vegetation and organic matter were consumed.

Materials and Methods

Hydrology

Hydrological investigations began in 1969 at the ELA, and the Lake 239 catchment was selected for detailed, long-term monitoring. A streamflow recording station was installed in the eastern subcatchment in 1972 and rebuilt immediately following the forest fire in 1974 (Fig. 1C, lower weir). Continuous records were kept each year from spring runoff in April until freeze-up in early November. Winter flow was estimated by interpolation between monthly field observations and examination of daily precipitation and air temperature records. During the flow season, the site was visited weekly to gather hydrological and precipitation data and to collect water chemistry samples. The upper weir (Fig. 1C) was constructed in 1973, and provided additional flow and chemistry data within the subcatchment. Daily rainfall and snowfall data were obtained from the nearby Lake 239 meteorological station (Beaty 1981, 1984; Beaty and Lyng 1989).

Bedload Collection

Bedload, suspended sediment, organic debris, and dissolved load are the products of erosion. Erosion is among the most difficult of hydrologic processes to measure, and bedload is the most difficult part of erosion to estimate (Hewlett 1982). The scarcity of published transport rates and particle sizes of bedload sediments largely reflects the lack of adequate techniques and devices for obtaining measurements over diverse flow conditions. This study used a properly sized and well-designed bedload sediment trap installed in the streambed. Regular and easy maintenance of the device was the key to its effective operation. The trap was sufficiently large to be left unattended for several days without overfilling with sediment, allowed easy sampling at any time or flow condition, and did not disturb the natural flow regime.

The trap (Fig. 2) consisted of a box measuring 1.2 × 2.4 × 0.5 m (capacity = 1.4 m^3) set into the sandy stream bottom so that the sill was at streambed elevation. Sides of the trap extended 0.5 m above the streambed to the top of the banks and were rigidly supported by a heavy wooden framework. Streamflow was diverted through two 30-cm-diameter culverts during sampling. Plywood doors with rubber gaskets, secured on bolt studs with large wing-nuts, sealed the two diversion channels. Similar sealed doors were fixed on the

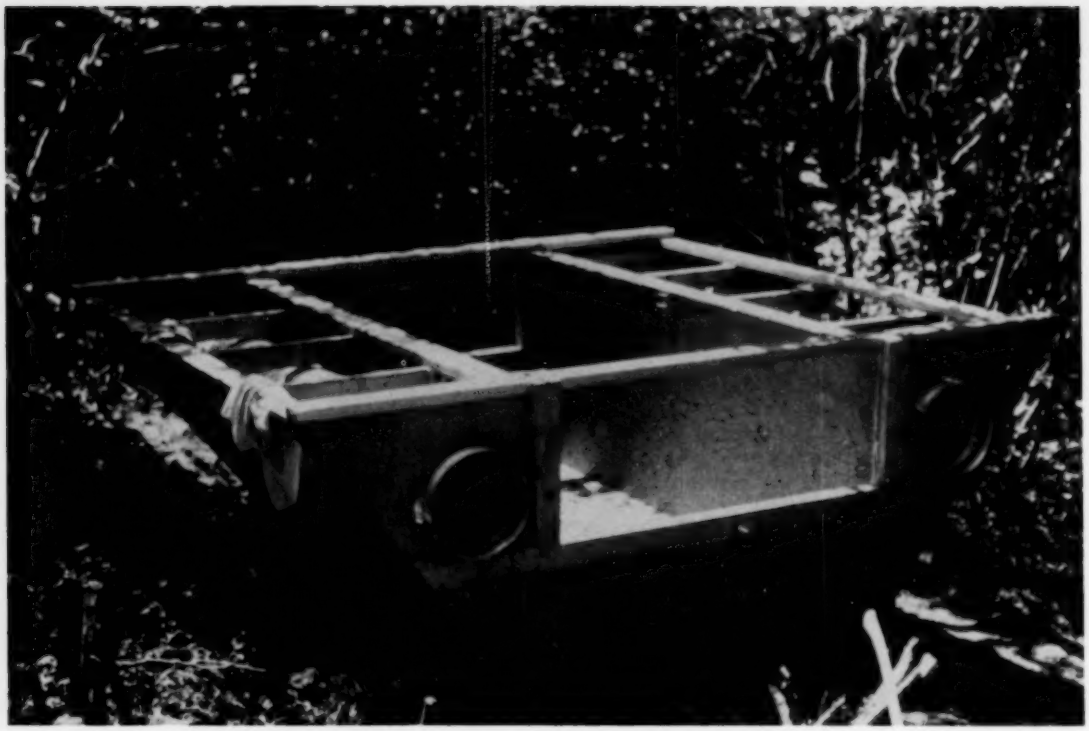


FIG. 2. Sediment bedload trap used in the Lake 239 eastern subcatchment stream.

front and rear of the trap to prevent seepage during sampling. Sandbags weighing 2300 kg on top of the diversion channels prevented the device from floating during sampling. A grid of 32 equal squares was marked along the sides of the trap and on a moveable plank so that the centre of each square could easily be located for measuring accumulated sediment depth.

The trap was installed on August 1, 1975. Bedload volume was estimated weekly, or during and after storms, by measuring sediment depth with a graduated measuring rod at the centre of each of the 32 grid squares in the trap. The volume of bedload material accumulated was calculated as the mean of these 32 depths times the surface area of the trap. Volume times dry density (2.50 $g \cdot cm^{-3}$; mean of six cores) yielded estimates of accumulated bedload expressed as dry weight.

To empty the trap, doors were bolted on the front and rear, and the two diversion culverts were opened to allow stream water to flow. Water inside the box was removed with a bucket to expose the sediment, which was then subsampled for grain size analysis and shovelled out. Once the trap was empty, the procedure was reversed to return it to normal operation.

Bedload samples for grain size analysis were sieved (Lambe 1951) and particle-size distributions were determined (Spangler 1966). Median diameter (maximum diameter of the smallest 50% of particles, by weight) and effective size (maximum diameter of the smallest 10% of particles, by weight) for each sample were determined from particle-size distribution curves to indicate changes in bedload composition over time. A low effective size indicates a sample with a large amount of fine material.

Suspended Sediment

Suspended sediment concentrations were measured to establish the relative importance of suspended load to bedload after recovery from the fires. Concentrations were characterized for base flow, the rising, peak, and recession segments of the runoff hydrograph. Depth-integrated replicate 1-L samples (sum = 154, 1978–90) were taken a few metres upstream of the bedload trap at the centre of the stream. Samples were filtered on Whatman GF/C glass fiber filters according to the methods described in Beaty (1981) and Campbell and Elliott (1975).

Water Chemistry

Water samples provided additional data useful for establishing the relative contributions of suspended, dissolved, and bedload components. Water samples were collected at least weekly during the flow season for all years and analyzed for dissolved and suspended chemical constituents (Stainton et al. 1977).

Results and Discussion

Flow Characteristics of the Eastern Subcatchment Stream

Streamflow in the eastern subcatchment was variable (Fig. 3); it was driven by the amount of snowpack in the catchment, the frequency and amount of rainfall, and moisture conditions prior to runoff. The rising and peak segments of rain-driven hydrographs lasted several hours whereas the recession limb lasted ≈5 d. Base flow was <0.015 $m^3 \cdot s^{-1}$ as determined from the analysis of storm hydrographs.

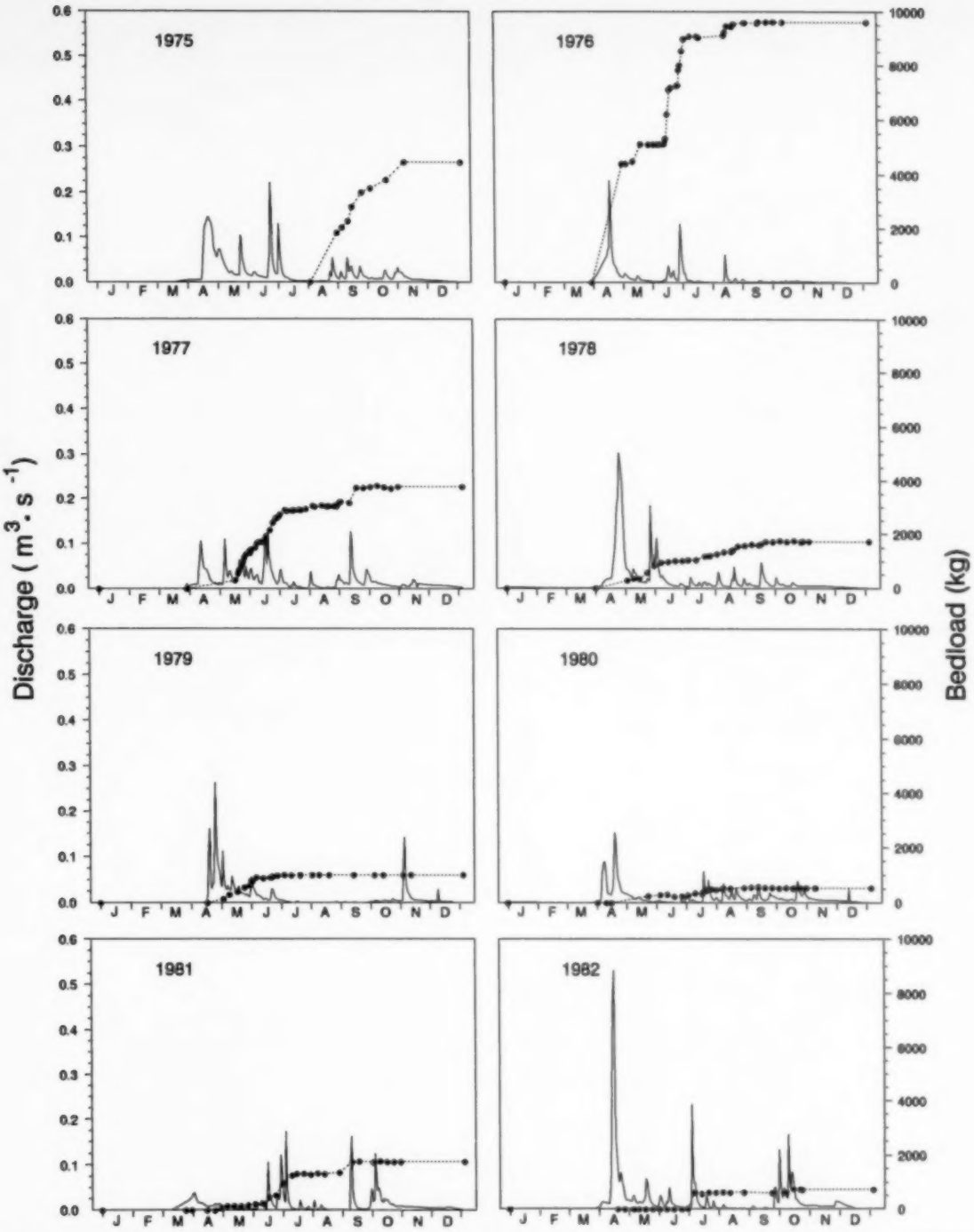


FIG. 3. Annual stream discharge hydrographs (mean daily values: $m^3 \cdot s^{-1}$) and cumulative bedload sediment transport (kg; dots), 1975–82. The 1975 panel does not include pre-August bedload material.

Basin antecedent moisture conditions determine the response to streamflow for a rainfall event, thereby contributing to the highly variable transport of material in streams. Runoff yield for identical rainstorms may vary according to antecedent moisture conditions and season (Newbury and Beaty 1980; Sidle 1988). For example, the hydrographs for four consecutive rainstorms in June and July 1981 are shown in Fig. 4. Rainfall in April (15.8 mm)

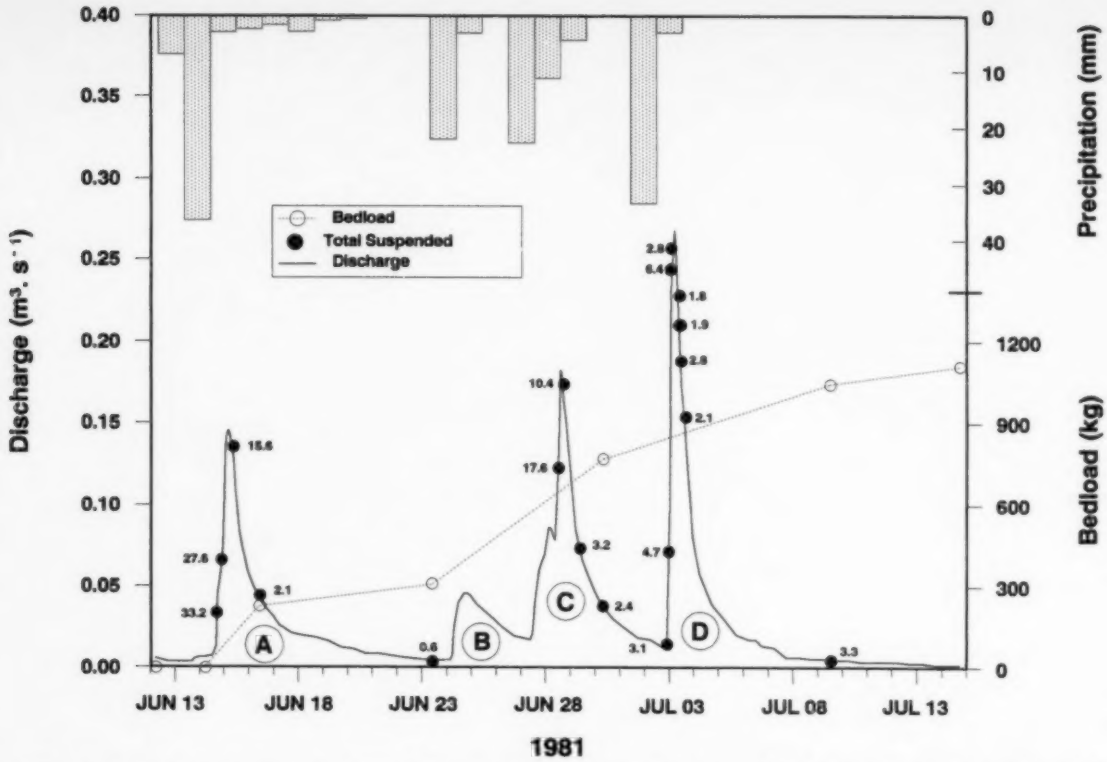


FIG. 4. Flow hydrographs for four consecutive rainfall events (A–D) with resulting suspended sediment concentrations and cumulative bedload data. Suspended sediment samples are located on the hydrograph according to time of sampling; concentrations are noted beside each point.

TABLE 1. Stream runoff and bedload transport rates for the eastern subcatchment of Lake 239 for defined periods between 1974 and 1982.

	Runoff (mm)	Precip. (mm)	Yield (%)[a]	Bedload mass (kg)[b]	Bedload rate (kg·mm^{-1})[c]	Precipitation (mm) >25 (d)[d]	Precipitation (mm) >12 (d)[e]
June 26/74 – Oct. 31/74	133	291	46	n/a[f]	n/a	2	8
Nov. 01/74 – Oct. 31/75	231	691	33	n/a	n/a	3	12
Aug. 01/75 – Oct. 31/75	60	225	27	4438	74.0	1	7
Nov. 01/75 – Oct. 31/76	143	500	29	9618	67.0	2	5
Nov. 01/76 – Oct. 31/77	232	701	33	3780	16.3	2	17
Nov. 01/77 – Oct. 31/78	299	767	39	1727	5.8	2	12
Nov. 01/78 – Oct. 31/79	155	568	27	1008	6.5	4	8
Nov. 01/79 – Oct. 31/80	188	579	32	543	2.9	2	10
Nov. 01/79 – June 19/80	105	198	53	240	2.3	0	0
June 20/80 – Oct. 31/80	83	380	22	303	3.7	2	10
Nov. 01/80 – Oct. 31/81	177	637	28	1798	10.2	6	14
Nov. 01/81 – Oct. 31/82	291	715	41	733	2.5	3	13

[a]Calculated basin yield (runoff/precipitation) for each period.
[b]Total bedload transport in kg for the defined period.
[c]Rate of bedload transport (kg·mm^{-1} of runoff).
[d]Number of calendar days that precipitation (May–Oct.) exceeded 25 mm.
[e]Number of calendar days that precipitation (May–Oct.) exceeded 12 mm.
[f]n/a = not available.

and May (19.4 mm) was well below the long-term averages of 44 and 65 mm for those months. This resulted in dry conditions leading up to the rainstorm period. Runoff yields for the four storms (minus base flow; see Linsley et al. 1949), 18, 17, 33, and 34% of rainfall, were initially low but gradually increased.

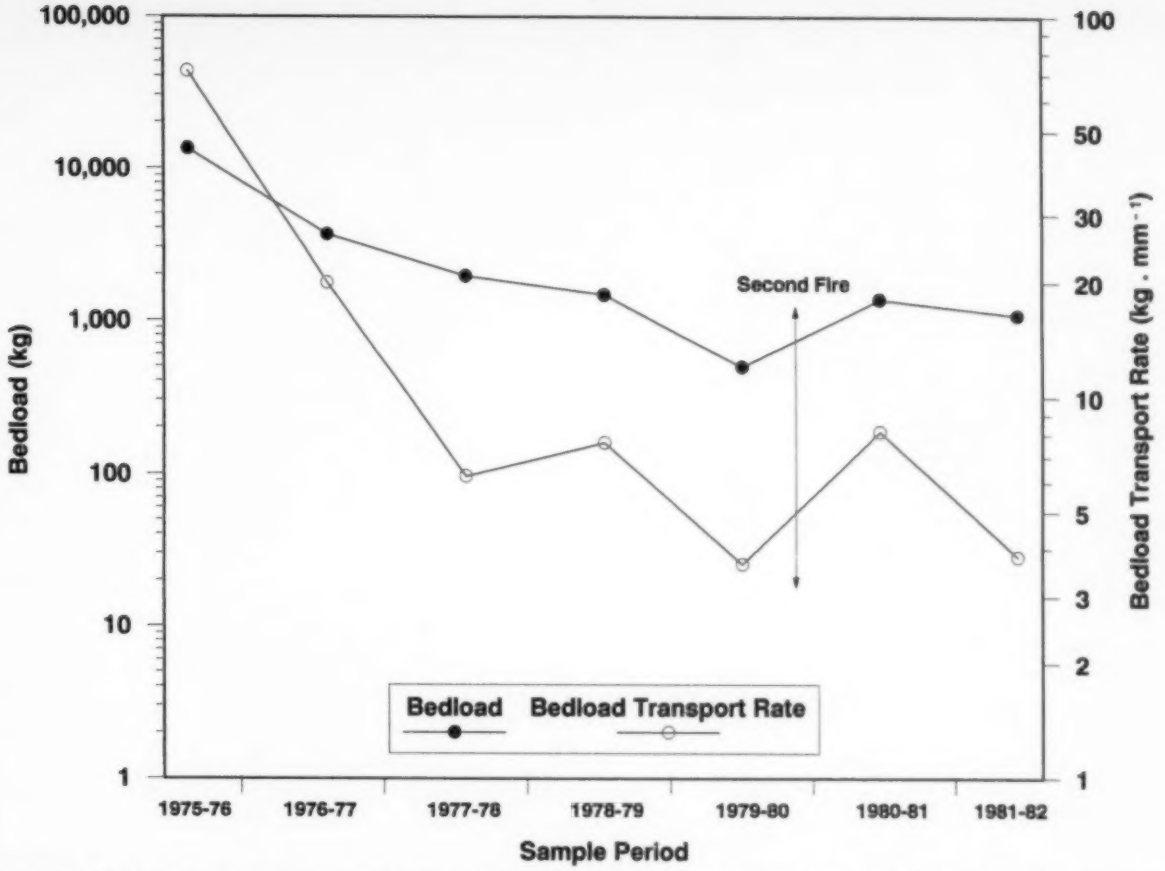


FIG. 5. Total bedload sediment transport (kg dry weight) and bedload transport rate ($kg \cdot mm^{-1}$ of runoff) for 1-yr periods (August 1 – July 31).

Bedload Transport

The bedload trap never overfilled; bedload movement was frequently observed at the full range of flow conditions, indicating successful operation of the trap. Bedload transport clearly increased in the years following the two forest fires in the eastern subcatchment (Fig. 3). Nearly 10 000 kg of material moved in 1976, but only 1728 kg of material moved in 1978, even though total precipitation was higher in 1978 (767 mm) than 1976 (500 mm) (Table 1; water year: Nov. 1 – Oct. 31). High bedload transport caused by the fire of 1974 is more evident when the data are expressed as a rate ($kg \cdot mm^{-1}$ of runoff) for defined time periods (Table 1; Fig. 5). By 1980, when the second fire occurred, the bedload transport rate had decreased dramatically, suggesting that the impact of the first fire lasted 5–6 yr.

The 1981 transport of material increased as a result of the 1980 fire but to a lesser extent than after the 1974 fire. This suggests that much of the available bedload material had already been removed from the subcatchment. Low masses of bedload were also measured in 1983 (471 kg), 1984 (39 kg), and 1985 (466 kg). Bedload material originated from the lower half of the subcatchment, because no bedload material was trapped at the upper weir.

Median diameter and effective size of bedload particles increased with time (Fig. 6). Fine material was flushed from the basin after the first fire, as indicated by increased amounts of coarse particles and decreased amounts of fine particles in the samples with time (Fig. 7). A 1-yr increase in the fine fraction was observed in 1980, following the second fire.

Total Suspended Solids

Concentrations of suspended sediment ranged from 0.01 to 74 $mg \cdot L^{-1}$ (Table 2). Concentrations depended on flow conditions at the time of sampling. Considerable variation within each segment was evident; the rising limb of the hydrograph was most variable (Fig. 4). In the four consecutive storm events shown in Fig. 4, the rising limb of the hydrograph had the highest concentrations of suspended sediment, and concentrations diminished over time. Concentrations during the rising limb decreased with each successive event probably because available material was removed from the subcatchment. Bedload transport increased over the period, demonstrating a lack of synchronization between the two processes.

Total suspended load was limited by availability of material rather than transport capacity of the stream. The highest suspended sediment concentration (74 $mg \cdot L^{-1}$) was recorded on September 23, 1982, on the rising limb of a storm event that followed a dry period of 7 wk. Virtually no bedload movement was observed at this time (Fig. 3).

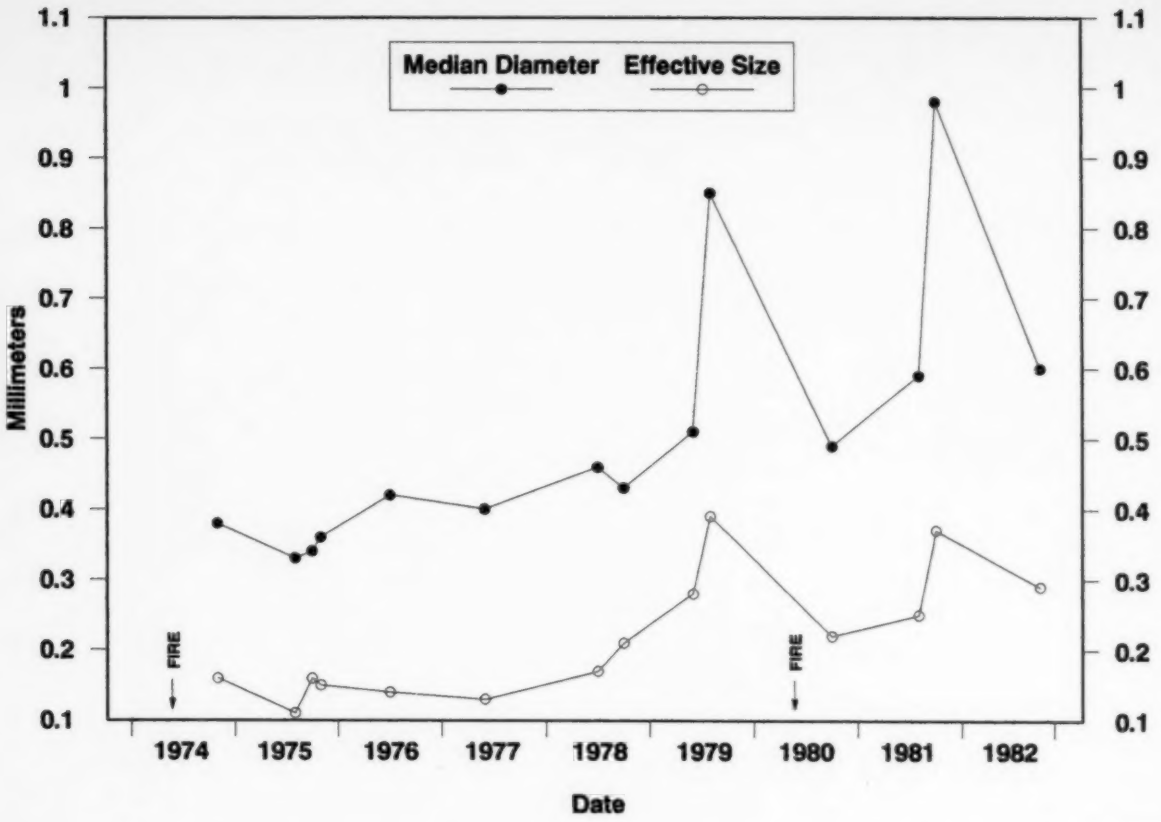


FIG. 6. Median diameter (mm) and effective particle size (mm) for 14 bedload samples collected from the eastern subcatchment stream of Lake 239 from 1974 to 1982.

TABLE 2. Total suspended sediment concentrations ($mg \cdot L^{-1}$) from the eastern subcatchment stream of Lake 239, 1978–90. Samples were categorized into four common segments of the runoff hydrograph.

	Hydrograph segment			
	Rising	Peak	Recession	Base flow
No. of samples	22	20	38	74
Maximum	73.89	16.19	6.02	3.59
Minimum	2.24	0.96	0.75	0.01
Mean	15.04	6.48	2.26	0.99
Standard deviation	17.41	5.18	1.09	0.75

TABLE 3. Estimated flow volumes and total suspended load in the east subcatchment stream of Lake 239 for 1982, according to hydrograph segment.

Hydrograph segment	Flow volume		Total suspended load	
	m^3	%	kg	%
Base flow	84 629	17	84	4
Rising limb	49 712	10	748	36
Peak segment	99 425	20	644	31
Recession limb	265 134	53	599	29
Total	498 900	100	2075	100

Mass Transport

The relative importance of bedload material to total sediment transport was determined for an average year, 1982, which was selected based on 20 yr of hydrological record (Beaty and Lyng 1989). Also, total bedload transport for 1982 (733 kg) was similar to estimated prefire levels.

Total suspended sediment (TSS) load for 1982 (2075 kg) was estimated by dividing total flow for the year into the four parts of the hydrograph and multiplying their individual volumes by the average concentrations of suspended sediment shown in Table 2. Base flow was estimated by summing daily flows in the base-flow range. The flow representing the rising, peak, and recession limbs was estimated by subtracting base flow from total flow. It was estimated, from Fig. 4, that the rising, peak, and recession segments of the hydrograph lasted 3, 3, and 94% of the time and accounted for 12, 24, and 64% of flow volume during non-base-flow conditions. The resulting flow volume and suspended sediment mass estimates are summarized in Table 3.

A duration analysis of mean daily flows for 1982 indicated that base flow occurred 78% of the time but accounted for only 17% of the flow volume and 4% of the suspended

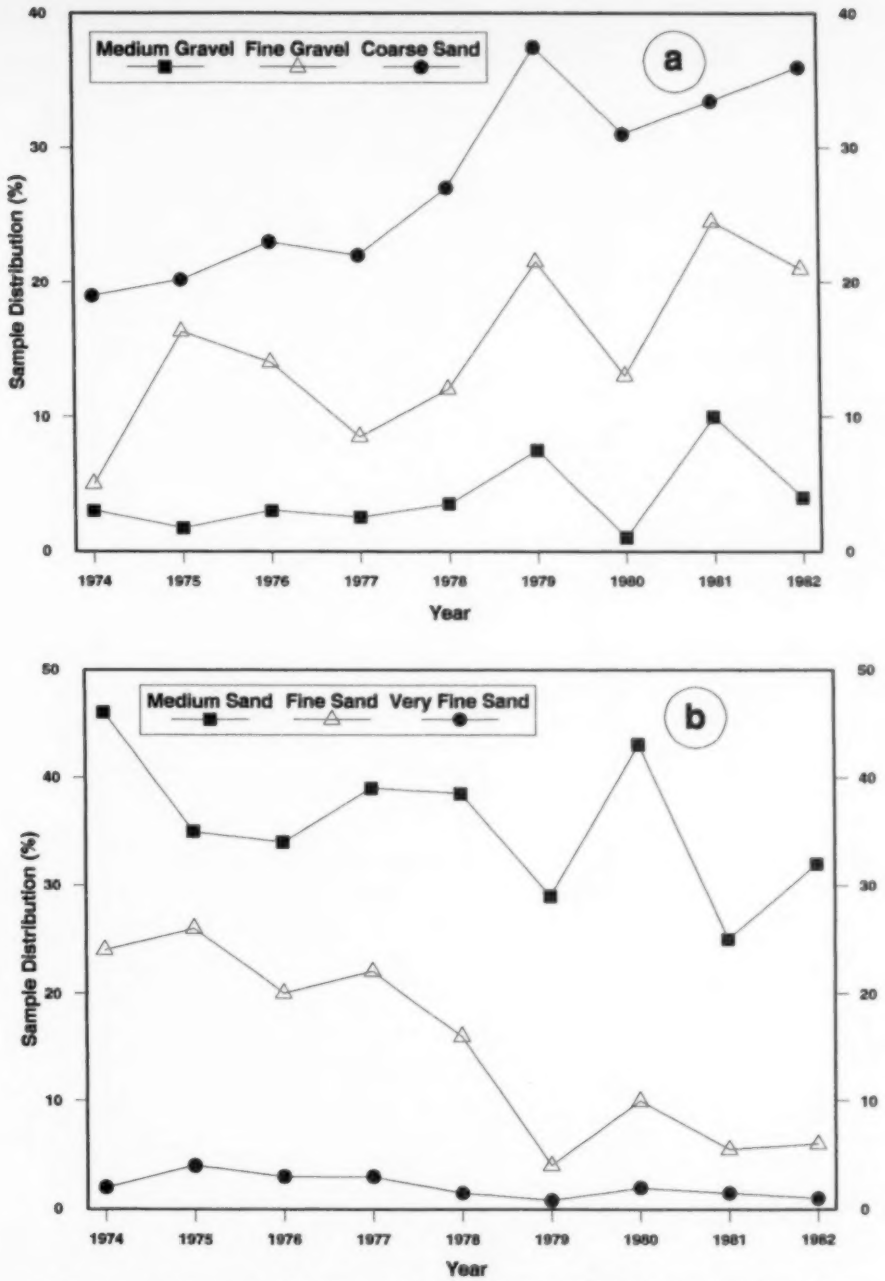


FIG. 7. Average percentage of (a) coarse and (b) fine fractions of bedload samples collected from the eastern subcatchment stream of Lake 239 from 1974 to 1982. Size ranges for each grade are according to Spangler (1966).

sediment (Table 3). Rising limbs occurred only ≈1% of the time, represented only 10% of the flow, and delivered the largest share of the suspended load (36%). Peak segments accounted for only 20% of the flow but 31% of the suspended sediment. Recession periods accounted for most of the total flow (53%) and 29% of the suspended sediment load.

Less sediment was transported in the spring runoff period than in rainfall-driven, major storm-flow events. An entire winter snowpack usually runs off over a period of ≈30 d, whereas a summer rainstorm, representing a similar volume of runoff, might occur in only 3–5 days. The daily spring freeze–thaw cycle causes diurnal fluctuations in streamflow, which prolongs runoff duration. As a result, spring peak

TABLE 4. Dissolved and suspended load (kg) for selected chemical constituents from the east subcatchment stream of Lake 239 for 1982.

Dissolved		Suspended	
DOC	8 468.4	C	1079.6
SO_4	3 433.6	N	70.9
Si	2 107.8	P	5.7
Ca	1 302.7		
DIC	1 221.2		
Na	679.2		
K	499.6		
Mg	425.2		
TDN	226.1		
Cl	208.6		
Fe	143.9		
Mn	26.8		
TDP	8.7		
H	1.0		
Total (kg)	18 752.8		1156.2

flow tend to be lower than for rainstorms, unless compounded by heavy spring rainfall. Also, stream banks in low-lying protected parts of the valley are frozen or armored by ice or snow, and they thaw late in the spring runoff period, reducing sediment delivery to the channel. Together, these factors contributed to little or no bedload transport and low concentrations of total suspended material (<3 $mg \cdot L^{-1}$ in five April samples) during the spring runoff period.

Chemical analyses for nutrients and most abundant ions allowed total dissolved export to be estimated. Total flow volume (from the day after the previous sample to the day of the sample) was multiplied by concentration of a variable to estimate the annual mass transport of dissolved load (Table 4).

Suspended nitrogen (N), carbon (C), and phosphorus (P), which represented most of the organic material in the TSS component, were estimated as described above (Table 4). Fifty-six percent of TSS was organic (1156 of 2075 kg; see Tables 3 and 4). Loss on ignition tests carried out on 36 TSS samples collected in 1982 averaged 45% (4.15 $mg \cdot L^{-1}$ before vs. 2.29 $mg \cdot L^{-1}$ after), which suggests that only considering suspended N, C, and P would underestimate the TSS load in the streamflow.

Schindler et al. (1992) reported increases in dissolved organic carbon (DOC) in Lake 239 during the same period as this study. Significant increases in runoff and in losses of N, P, and potassium followed the 1974 fire (Schindler et al. 1980). Bayley et al. (1992a) further reported that water yields and concentrations of all forms of N and P in stream water increased and that, in general, N losses partially recovered 5–6 yr after the fire, whereas P losses returned to normal in 2–3 yr. Weaker but distinct increases occurred after the second fire. Analyses of suspended N, C, and P in the study by Bayley et al. (1992a) suggested that the concentrations of TSS increased as a result of fire.

The mass-transport budget calculated for 1982 showed that the bedload (733 kg) and suspended components (2075 kg) were relatively minor compared with dissolved load (18 753 kg) in an average precipitation year. Thus, material transport was 87% dissolved, 10% suspended, and only 3% bedload.

An inability to adequately sample and quantify organic debris in the streamflow was a shortcoming of the study. The presence of large organic debris in the flow was evident, especially during rainstorm events. A large conical net, sewn from a piece of knotless nylon fishing net material (5-mm mesh), was used to collect variable but substantial amounts of organic debris composed of branches, leaf and pine needle litter, and occasionally dead animals (insects, frogs, snakes, and small rodents). Organic debris may be an important part of total material mass transport in a stream and should be considered in future studies.

In summary, bedload material in the eastern subcatchment of Lake 239 was easily measured once an effective trap design and sampling method were established. Bedload traps can successfully measure bedload movement in small streams providing that the trap is big enough, and the bedload is frequently measured and emptied.

Bedload transport is variable because several small events may make sediment available to the stream for movement during a major storm. For this reason, Sidle (1988) questioned the segregation of rising and falling limbs of storm hydrographs in empirical bedload models.

Results of the study showed that the initial forest fire increased bedload transport ≈20 times. Bedload transport rates diminished after 6 yr to prefire rates because of the reestablishment of protective vegetative cover. The second fire only increased bedload transport approximately three times. Median particle sizes were smallest just after the 1974 fire, and increased over time.

Concentrations of TSS varied greatly during storm runoff. A brief period occurred shortly before the peak of the hydrograph during which time material was washed out of the subcatchment; peak concentrations were often an order of magnitude higher than for other segments of the hydrograph. Average suspended sediment concentrations were highest on the rising limb of the hydrograph and declined progressively from the peak segment to the recession limb to the base-flow condition. Little can be said about the effect of the 1974 fire on the transport of suspended sediment because the collection of samples did not begin until 1978.

Finally, global warming may have considerable impact on sediment yields from stream catchments in northwestern Ontario. For example, lightning is a major cause of forest fires (Price and Rind 1991). Increased temperature, evaporation, and convection caused by global warming may result in increased lightning activity and wildfire frequency (Price and Rind 1991). Future forest fires may burn with greater intensity (Lanoville 1990), thereby increasing sediment yield (Robichaud and Waldrop 1994).

Acknowledgments

I thank D. Schindler who had the foresight to encourage this study. R. Newbury shared his many ideas in the early stages of the study. P. Michaelis and R. Reid helped build and install the bedload trap. A. Dalton, L. Mohr, P. Crawford, W. Dentry, D. Rystephanuk, K. Downey, A. Solinske, and J. Millman provided summer assistance. M. Lyng and N. Strange helped produce the figures, and D. Laroque did much of the word processing. P. Campbell, G. McCullough, D. Cobb, C. Katopodis, D. Schindler, and D. Rosenberg provided valuable comments.

References

BAYLEY, S.E., D.W. SCHINDLER, K.G. BEATY, B.R. PARKER, AND M.P. STAINTON. 1992a. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorus. Can. J. Fish. Aquat. Sci. 49: 584–596.

BAYLEY, S.E., D.W. SCHINDLER, B.R. PARKER, M.P. STAINTON, AND K.G. BEATY. 1992b. Effects of forest fire and drought on acidity of a base-poor boreal forest stream: similarities between climatic warming and acidic precipitation. Biogeochemistry 17: 191–204.

BEATY, K.G. 1981. Hydrometeorological data for the Experimental Lakes Area, northwestern Ontario, 1969 through 1978 (in three parts). Can. Data Rep. Fish. Aquat. Sci. 285: 1–367.

BEATY, K.G. 1984. Hydrometeorological data for the Experimental Lakes Area, northwestern Ontario, 1979–1981. Can. Data Rep. Fish. Aquat. Sci. 480: 146 p.

BEATY, K.G., AND M.E. LYNG. 1989. Hydrometeorological data for the Experimental Lakes Area, northwestern Ontario, 1982 to 1987. Can. Data Rep. Fish. Aquat. Sci. 759: 280 p.

BOTTOMLEY, D. 1974. Influence of hydrology and weathering on the water chemistry of a small Precambrian Shield watershed. M.Sc. thesis, University of Waterloo, Waterloo, ON. 118 p.

BRADBURY, J.P., S.J. TARAPCHAK, J.C.B. WADDINGTON, AND R.F. WRIGHT. 1975. The impact of a forest fire on a wilderness lake in northeastern Minnesota. Int. Ver. Theor. Angew. Limnol. Verh. 19: 875–883.

BROWN, J.A.H. 1972. Hydrologic effects of a bushfire in a catchment in south-eastern New South Wales. J. Hydrol. 15: 77–96.

BRUNSKILL, G.J., AND D.W. SCHINDLER. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 139–155.

CAMPBELL, P., AND S. ELLIOTT. 1975. Assessment of centrifugation and filtration as methods for determining low concentrations of suspended sediment in natural waters. Can. Fish. Mar. Serv. Res. Dev. Tech. Rep. 545: 18 p.

CHOW, V.T. 1964. Handbook of applied hydrology. McGraw-Hill, New York. 1418 p.

CORDONE, A.J., AND D.W. KELLY. 1961. The influences of inorganic sediment on the aquatic life of streams. Calif. Fish Game 47: 189–228.

CULP, J.M., F.J. WRONA, AND R.W. DAVIES. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. Can. J. Zool. 64: 1345–1351.

ELLIS, M.M. 1936. Erosion silt as a factor in aquatic environments. Ecology 17: 29–42.

FUDGE, R.J.P., AND R.A. BODALY. 1984. Postimpoundment winter sedimentation and survival of lake whitefish (*Coregonus clupeaformis*) eggs in Southern Indian Lake, Manitoba. Can. J. Fish. Aquat. Sci. 41: 701–705.

HEWLETT, J.D. 1982. Principles of forest hydrology. University of Georgia Press, Athens, GA. 183 p.

JOHNSON, W.E., AND J.R. VALLENTYNE. 1971. Rationale, background and development of experimental lake studies in northwestern Ontario. J. Fish. Res. Board Can. 28: 123–128.

KENNEDY, K. 1974. Geohydrology and hydrochemistry of a small Precambrian Shield watershed. M.Sc. thesis, University of Waterloo, Waterloo, ON. 248 p.

LAMBE, T.W. 1951. Soil testing for engineers. John Wiley and Sons, New York. 165 p.

LANOVILLE, R. 1990. Effects of global warming on forest fire management in the northwest territories, p. 117–121. *In* G. Wall and L. Weber [ed.] Proceedings of the Fourth Meeting on Northern Climate, October 17–18, 1990, Yellowknife, NT. Canadian Climate Program, Atmospheric Environment Service, Environment Canada, Downsview, ON.

LEMLY, A.D. 1982. Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. Hydrobiologia 87: 229–245.

LINSLEY, R.K., M.A. KOHLER, AND J.L.H. PAULHUS. 1949. Applied hydrology. McGraw-Hill, New York. 689 p.

MCCULLOUGH, G.K., AND P. CAMPBELL. 1993. Lake variation and climate change study: ELA lakes, 1986–1990. II. Watershed geography and lake morphology. Can. Tech. Rep. Fish. Aquat. Sci. 1898: 29 p.

NEWBURY, R.W., AND K.G. BEATY. 1977. Water budgets in small Precambrian lake basins in northwestern Ontario, Canada, p. 132–139. *In* Second Conference on Hydrometeorology, October 25–27, 1977, Toronto, ON. American Meteorological Society, Boston, MA.

NEWBURY, R.W., AND K.G. BEATY. 1980. Water renewal efficiency of watershed and lake combinations in the ELA region of the Precambrian Shield. Can. J. Fish. Aquat. Sci. 37: 335–341.

PETERS, J.C. 1967. Effects on a trout stream of sediment from agricultural practices. J. Wild. Manage. 31: 805–812.

PRICE, C., AND D. RIND. 1991. Lightning activity in a greenhouse world, p. 598–604. In P.L. Andrews and D.F. Potts [ed.] Proceedings of the 11th Conference on Fire and Forest Meteorology, April 16–19, 1991, Missoula, MT. Society of American Foresters and American Meteorological Society, Bethesda, MD.

RAE, J.G. 1987. The effects of flooding and sediments on the structure of a stream midge assemblage. Hydrobiologia 144: 3–10.

ROBICHAUD, P.R., AND T.A. WALDROP. 1994. A comparison of surface runoff and sediment yields from low- and high-severity site preparation burns. Water Resour. Bull. 30: 27–34.

SCHINDLER, D.W., S.E. BAYLEY, P.J. CURTIS, B.R. PARKER, M.P. STAINTON, AND C.A. KELLY. 1992. Natural and man-caused factors affecting the abundance and cycling of dissolved organic substances in Precambrian Shield lakes. Hydrobiologia 229: 1–21.

SCHINDLER, D.W., R.W. NEWBURY, K.G. BEATY, AND P. CAMPBELL. 1976. Natural water and chemical budgets for a small Precambrian lake basin in central Canada. J. Fish. Res. Board Can. 33: 2526–2543.

SCHINDLER, D.W., R.W. NEWBURY, K.G. BEATY, J. PROKOPOWICH, T. RUSZCZYNSKI, AND J.A. DALTON. 1980. Effects of a windstorm and forest fire on chemical losses from forested watersheds and on the quality of receiving streams. Can. J. Fish. Aquat. Sci. 37: 328–334.

SHAHLAEE, A.K., W.L. NUTTER, E.R. BURROUGHS, JR., AND L.A. MORRIS. 1991. Runoff and sediment production from burned forest sites in the Georgia Piedmont. Water Resour. Bull. 27: 485–493.

SIDLE, R.C. 1988. Bed load transport regime of a small forest stream. Water Resour. Res. 24: 207–218.

SPANGLER, M.G. 1966. Soil engineering. 2nd ed. International Text Book Co., Scranton, PA. 483 p.

STAINTON, M.P., M.J. CAPEL, AND F.A.J. ARMSTRONG. 1977. The chemical analysis of fresh water. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25: 180 p.

TEBO, L.B., JR. 1955. Effects of siltation, resulting from improper logging, on the bottom fauna of a small trout stream in the southern Appalachians. Prog. Fish-Cult. 17: 64–70.

TELLER, J.T. 1985. Glacial Lake Agassiz and its influence on the Great Lakes, p. 1–16. In P.F. Karrow and P.E. Calkin [ed.] Quaternary evolution of the Great Lakes. Spec. Pap. 30. Geological Association of Canada, St. John's, NF.

Sensitivity of Estimates of Seasonal Phytoplankton Photosynthesis to Sampling Frequency[1]

E.U. Schindler, E.R. DeBruyn,[2] E.J. Fee, and J.A. Shearer

Department of Fisheries and Oceans, Freshwater Institute Science Laboratory, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Schindler, E.U., E.R. DeBruyn, E.J. Fee, and J.A. Shearer. 1994. Sensitivity of estimates of seasonal phytoplankton photosynthesis to sampling frequency. Can. J. Fish. Aquat. Sci. 51: 2734–2738.

Phytoplankton photosynthesis was monitored once or twice weekly in an oligotrophic Canadian Shield lake in northwestern Ontario during the ice-free season for 6 yr. These data sets were subsampled in various ways to determine how the precision of estimates of ice-free season phytoplankton photosynthesis was affected by sampling frequency. Deviations were as large as 20% if a measurement was not taken before thermal stratification was established in the spring, or if samples were taken at monthly intervals during the ice-free season. Shorter sampling intervals (1, 2, and 3 wk were tested) all resulted in deviations of about 10%. Taking samples irregularly (every day for the 3 d subsequent to rainfall events ≥5 mm) instead of at regular time intervals did not reduce deviations.

On a surveillé une ou deux fois par semaine la photosynthèse chez le phytoplancton d'un lac oligotrophe du Bouclier canadien dans le nord-ouest de l'Ontario au cours de la saison où les eaux sont libres de glace durant 6 ans. Des sous-échantillons divers ont été établis dans les ensembles de données ainsi obtenus de façon à ce qu'on puisse déterminer dans quelle mesure la précision des estimations de la photosynthèse phytoplanctonique durant la saison sans glace était tributaire de la fréquence d'échantillonnage. Les écarts pouvaient être de 20% si les mesures n'étaient pas effectuées avant l'établissement de la stratification thermique au printemps, ou si l'intervalle d'échantillonnage était d'un mois. Avec des intervalles d'échantillonnage plus courts (1, 2 et 3 semaines), les écarts se situent dans tous les cas autour de 10%. Le prélèvement d'échantillons à intervalles irréguliers (chaque jour durant les 3 jours qui suivent une pluie de 5 mm ou plus) plutôt qu'à intervalles réguliers n'a pas eu pour effet de réduire les écarts.

Received July 19, 1993
Accepted July 12, 1994
(J12014)

Reçu le 19 juillet 1993
Accepté le 12 juillet 1994

Ice-free season rates of phytoplankton photosynthesis (PP) have been measured in many lakes at the Experimental Lakes Area (ELA) in northwestern Ontario (Johnson and Vallentyne 1971) for more than 20 yr (Fee 1979; Fee et al. 1982; DeBruyn et al. 1982, 1984; E. DeBruyn, J. Shearer, and E. Schindler, unpublished data). In the method used at the ELA (Shearer et al. 1985; Fee 1990), samples are taken regularly during the ice-free season; chlorophyll and the parameters of the photosynthesis versus light curve provide input to a numerical model that simulates in situ PP at daily intervals by interpolating the photosynthetic parameters linearly between sampling dates and using semicontinuous measurements (30-min averages) of solar irradiance. Whole-lake ^{14}C additions (Bower et al. 1987) and comparisons with in situ measurements and simulated in situ measurements (Fee 1973; Harrison et al. 1985; Lohrenz et al. 1992) have shown that this method gives accurate estimates of daily areal photosynthesis, but no estimate of the accuracy of seasonal estimates is available.

One variable that should affect the accuracy of seasonal PP estimates is the number of times that measurements are made during the growing season. Vollenweider's (1969) suggestion that samples be taken at 15- to 30-d intervals or less has been widely followed: Harrison and Platt (1980) and Asov (1986) sampled every 2 wk, Malone (1982) sampled every month, Bakker et al. (1990) sampled every week, and Rodhe et al. (1956) sampled daily and weekly. However, Vollenweider offered no reason why samples should be taken every 15–30 d; because Rodhe et al. (1956) found variations of PP from one day to the next, it could just as well be argued that daily sampling is required. No studies exist that have determined the relationship between the time interval between repeated sampling of a water body and the accuracy of seasonal PP estimates.

Another variable that may influence the accuracy of seasonal PP estimates in temperate zone lakes is how soon sampling is initiated after ice melt in the spring. Algal biomass is frequently greatest immediately after ice-out (Wetzel 1975); missing this pulse could thus affect seasonal PP estimates. Vollenweider (1969) did not mention this variable, and few published studies explicitly state when sampling was initiated relative to ice-out.

Finally, because algal growth in most natural lakes is nutrient limited (Healey and Hendzel 1980), and because direct precipitation on the surface of the lake is the main source of nutrients to small, natural Canadian Shield lakes (Schindler and Nighswander 1970; Bayley et al. 1992), it might be expected that measuring PP at regular intervals throughout the growing season would give a significantly different result than taking samples irregularly, i.e., in synchrony with rainfall events. Indeed, Mallin et al. (1991) found that nutrient input from rainfall caused photosynthesis pulses.

[1]This paper is one of a series done in honour of the 25th anniversary of the Experimental Lakes Area.

[2]Present address: Department of Fisheries and Oceans, Bayfield Institute, 867 Lakeshore Rd., Box 5050, Burlington, ON L7R 4A6, Canada.

TABLE 1. Ice-out dates, sampling start dates, and stratification dates for the years of intensive sampling.

Year	Ice-out date	Sampling start date	Stratification date
1973	May 01	May 02	May 21
1974	May 09	May 10	May 10
1975	May 07	May 08	May 13
1976	April 23	April 29	April 29
1988	April 30	May 02	May 09
1989	May 11	May 15	May 15

TABLE 2. Number of samples used in various sampling scenarios derived from the complete data sets to calculate seasonal phytoplankton photosynthesis. ns = scenario could not be constructed.

Scenario	1973	1974	1975	1976	1988	1989
1[a]	35	29	28	28	50	36
2[b]	28	26	26	22	23	22
3[c]	14	13	14	12	13	12
4[d]	8	8	8	7	7	7
5[e]	ns	15	ns	ns	13	12
6[f]	1	ns	14	12	13	12
7[g]	7	8	7	7	7	7
8[h]	ns	ns	ns	ns	18	21
9[i]	ns	ns	ns	ns	16	15
10[j]	ns	ns	ns	ns	12	11
11[k]	10	9	10	9	9	9
12[l]	12	10	ns	10	10	9
13[m]	12	11	11	12	12	11

[a]Complete data set.
[b]Weekly from ice-out.
[c]Every 2 wk from ice-out.
[d]Monthly from ice-out.
[e]Every 2 wk starting before stratification.
[f]Every 2 wk starting after stratification.
[g]Monthly starting after stratification.
[h]Episodic with emphasis at precipitation episodes >5.0 mm.
[i]Early high-frequency sampling (every 3 d) and every 2 wk after first month.
[j]Early high-frequency sampling (every 3 d) and monthly after first month.
[k]Every 3 wk after ice-out.
[l]Weekly from time of ice-out until full stratification and every 3 wk thereafter.
[m]Every week until first week of June and every 3 wk thereafter.

In this paper, we empirically investigate how seasonal PP estimates are affected by different sampling frequencies. We do this by analyzing various subsets of data from years when photosynthesis measurements were made more frequently than usual: at least once weekly in 1973–1976 and at least twice weekly in 1988–1989.

Methods

Lake 239 (49°45′N, 93°45′W) is a typical oligotrophic ELA lake. It is 56 ha in surface area, has a maximum depth of 30 m (Brunskill and Schindler 1971, fig. 9) and a mean water renewal time of 10 yr (K. Beaty, Department of Fisheries and Oceans, Winnipeg, MB, personal communication). Seasonal rates of PP have been measured for >20 yr in

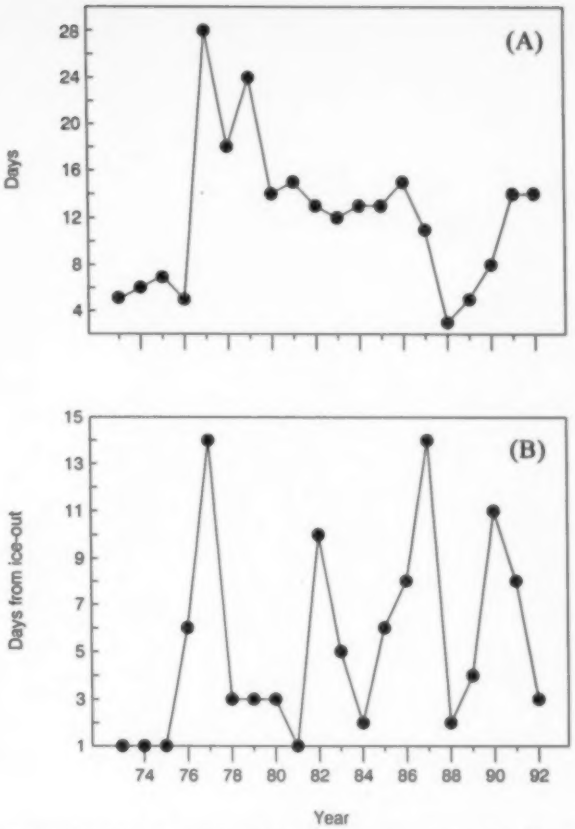


FIG. 1. (A) Mean time interval (days) between samples. (B) Number of days after ice-out when first sample was taken.

Lake 239; interseasonal variations of PP in the lake are similar to variations observed in other unmanipulated lakes in the ELA (Schindler et al. 1990). Ice-free season PP comprises approximately 95% of the annual total (Shearer et al. 1985) primarily because small lakes are covered by about 25 cm of snow during the winter, which prevents light from reaching the water column. Most underice PP occurs in the last month before ice-out when snow has melted and photosynthetically available radiation (PAR, the total number of quanta between 400 and 700 nm) is high. On large lakes or ones at high latitudes, underice PP can be a high percentage of the annual total because large lakes are often thinly covered with snow, and lakes at high latitudes are ice covered in May and June but have long daylight periods (Shearer et al. 1985).

During the ice-free seasons of 1973–1976, Lake 239 was sampled at least once a week and, during the ice-free seasons of 1988 and 1989, it was sampled approximately every 3 d from ice-out to mid September. In 1988 and 1989, samples were also taken every day during the 3 d after every major precipitation event (≥5 mm, an arbitrarily chosen value), after which the 3-d interval was resumed. Table 1 contains the ice-out dates (K. Beaty, personal communication), sampling start dates, and stratification dates of Lake 239 in the years of intensive study. On each sampling date, both the mixed layer and metalimnion were sampled. The metalimnetic layer was sampled from the "bottom" of the mixed layer

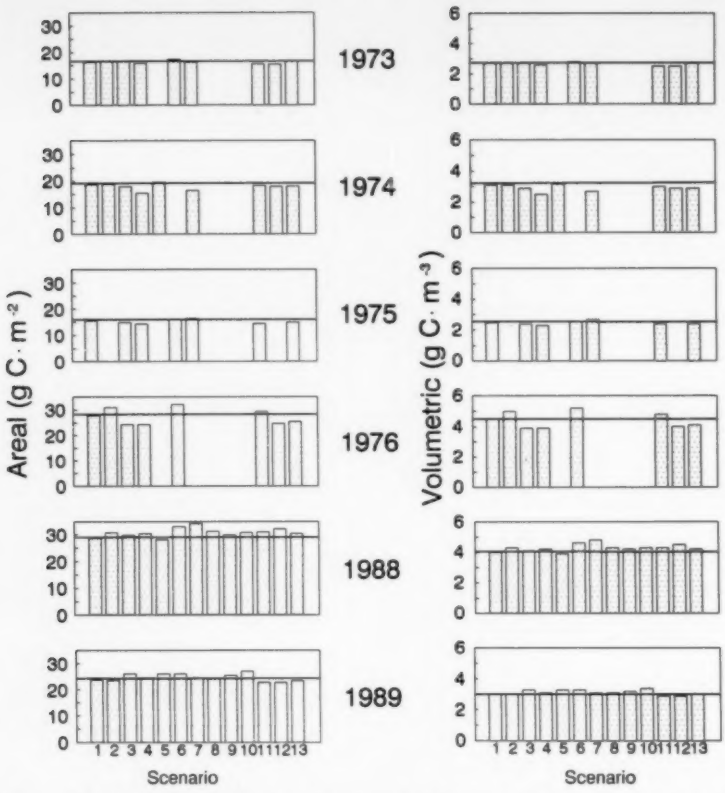


FIG. 2. Rates of seasonal phytoplankton photosynthesis (areal and volumetric) for different scenarios (see Table 2 for a description of each scenario).

(the first sharp inflection of the temperature–depth curve, normally >1°C·m^{-1}) down to the depth where 0.5% of the surface irradiance occurred. From 1973 – August 1974, samples were taken at discrete depths within each layer (Shearer and Fee 1974; Shearer 1976); at all other times a sampler that integrated continuously (Shearer 1978) was used.

Samples were returned to the laboratory within 30 min of collection and were processed under low light conditions to avoid light shock. ^{14}C was used for determining carbon uptake. Laboratory procedures used from 1973–1976 were described in Shearer and Fee (1974), Shearer (1976), DeClercq and Shearer (1976), and DeClercq et al. (1977). In 1988 and 1989, laboratory procedures followed Shearer et al. (1985), except that a single aliquot of inorganic ^{14}C was added to a subsample that was mixed and then siphoned into 60-mL Pyrex bottles; this procedure reduced interbottle variance by eliminating pipetting errors.

Seasonal PP was calculated with a computer program (Fee 1990) using actual solar irradiances: the surface PAR observed at the ELA field station during each year. The program produced estimates of photosynthesis both per unit of lake surface area and per unit volume of the euphotic zone. All estimates were corrected for the decrease of lake volume with depth (Fee 1980). If a date was missing from the PAR seasonal data, 70% of the simulated cloud-free values were used; this is the percentage of possible PAR that occurs on an "average" day at the ELA (Shearer et al. 1985). The program also calculates mean PAR in the water column from surface PAR, mixing depth, and light extinction over depth and the decrease of waterbody volume with depth; these means refer to the entire 24-h day. Finally, PP and mean PAR in the water column are calculated separately for the layers above and below the thermocline.

The complete data set for each year is considered the parent data set and is referred to as scenario 1. The parent data set was subsampled to create several sampling scenarios (Table 2), and the seasonal rate of PP for each of these sampling scenarios was calculated. Apart from the episodic scenario, which was designed to examine the effect of irregular nutrient inputs from precipitation events on PP, scenarios closely mimicked sampling schedules used on the lake in years of less intensive sampling. The deviation (D), calculated as a percentage, for each scenario relative to the parent data set was calculated by $D = 100(PP_{subset} - PP_{parent})/PP_{parent}$.

Results and Discussion

At ELA, Lake 239 was sampled at time intervals varying from 1 wk to 1 mo, depending on the resources available in any given year (Fig. 1A). The first sample was taken within 1 wk of the ice-out date (Fig. 1B) in 14 of the 20 yr, but in some years (e.g., 1987, when ice-out was unusually early) sampling started 2 wk after ice-out. The rates of seasonal photosynthesis, both square metres of lake surface and cubic metres of the euphotic zone for each of the scenarios, are illustrated in Fig. 2. The Ds were similar when examined

TABLE 3. Percent deviation of different scenarios of phytoplankton photosynthesis relative to the complete data set (scenario 1) for both areal and volumetric calculations (see Table 2 for description of scenarios).

Status[a]	Sample frequency[b]	Scenario	1973	1974	1975	1976	1988	1989	Mean[c]
				% areal deviation					
B	1	2	1.2	0.5	0.0	11.2	7.0	−0.4	3.4
B	2	3	1.2	−4.8	−3.9	−12.6	3.5	9.7	5.9
B	4	4	−3.1	−18.1	−7.7	−13.0	5.6	3.8	8.5
B	2	5		4.3			−2.5	9.7	5.5
A	2	6	6.1		3.2	15.1	15.0	9.7	9.8
A	4	7	0.0	−12.2	5.8	−13.0	19.9	3.8	9.1
	Episodic	8					8.7	1.7	5.2
B	2	9					4.2	7.1	5.7
B	4	10					7.0	13.9	10.4
B	3	11	−4.3	−2.7	−6.5	5.4	7.7	−4.2	5.1
B	3	12	−4.9	−4.8		−11.5	12.2	−4.2	7.5
B	3	13	3.1	−3.7	−3.9	−8.6	5.6	−1.3	4.4
				% volumetric deviation					
B	1	2	0.0	0.0	0.0	11.1	7.5	0.0	3.1
B	2	3	0.0	−6.5	−4.0	−13.3	−2.5	10.0	6.0
B	4	4	−3.7	−19.4	−8.0	−13.3	5.0	3.3	8.8
B	2	5		3.2			2.5	10.0	5.2
A	2	6	3.7		4.0	15.6	15.0	10.0	9.7
A	4	7	0.0	−12.9	8.0	−13.3	20.0	3.3	9.6
	Episodic	8					7.5	3.3	5.4
B	2	9					5.0	6.7	5.8
B	4	10					7.5	13.3	10.4
B	3	11	−7.4	−3.2	−4.0	6.7	7.5	−3.3	5.4
B	3	12	−7.4	−6.5		−11.1	12.5	−3.3	8.2
B	3	13	0.0	−6.5	−4.0	−8.9	5.0	0.0	4.1

[a]A = sampling was started after stratification was established; B = sampling was started before stratification was established.
[b]Sample frequency = time interval in weeks between sampling events.
[c]Mean is calculated by treating all numbers as positive.

areally as well as volumetrically (Table 3) and were both positive and negative. The majority of the *D*s for all 6 yr for all scenarios were on the order of 5–10%, which is similar to laboratory analytical errors (Shearer et al. 1985). The highest deviations (15–20%) resulted from sampling at monthly intervals or initiating sampling after stratification was established in the spring, which probably resulted from missing the spring phytoplankton pulse. The *D*s associated with episodic sampling (scenario 8) approximated those of scenarios in which sampling intervals were equally spaced. Based on these results, interannual or interlake differences in seasonal photosynthesis >20% can be interpreted as actual differences (i.e., not methodological artifacts).

Rodhe et al. (1956) found high variation in in situ PP rates from one day to the next in Lake Erken and they recommended that samples be taken more frequently than once a week; this conclusion is not supported by our results. Lake Erken is eutrophic and has chlorophyll concentrations ranging from 50–470 $\mu g \cdot L^{-1}$; by comparison, chlorophyll in Lake 239 ranged from 1.0–11 $\mu g \cdot L^{-1}$. Rodhe et al. (1956) attributed the high variability to short-term fluctuations in the horizontal distribution of phytoplankton because of irregular mixing of nutrient-rich metalimnetic water, into the epilimnion. However, because these authors sampled at discrete depths, they could have oversampled chlorophyll "peaks" in the water column. In addition, eutrophic lakes are more temporally variable than oligotrophic ones (Fee et al. 1991); thus, results from Lake Erken are not comparable to those from oligotrophic Lake 239. Finally, the in situ method used by Rodhe et al. (1956) is notoriously sensitive to daily variations of cloudiness; consequently, it is impossible to determine how much of the variation is a result of biological variability.

Vollenweider's (1969) recommendation that samples should be taken at 15- to 30-d intervals is generally supported by our results. However, 30-d (monthly) intervals are probably too long, because they resulted in the highest *D*s. All shorter intervals produced *D*s on the order of 5–15%, provided that sampling was initiated shortly after ice-out; this is probably the best that can be accomplished using current methods. Higher frequency sampling is not justified because the increased labour or resources involved do not substantially reduce *D*s.

We conclude that good estimation of seasonal PP in temperate lakes depends on obtaining a sample before stratification is established in the spring. For greatest accuracy, samples should be taken more frequently than monthly during the ice-free season; however, it seems to be of little importance whether samples are taken weekly, every 2 wk, or every 3 wk. It is important to qualify this conclusion by noting that it only applies to oligotrophic water bodies and ones that have long water renewal times (>5 yr). Eutrophic

systems are much more temporally variable (Marshall and Peters 1989; Fee et al. 1991) and would thus require higher frequency sampling for an equivalent degree of accuracy.

Acknowledgements

M. Boone, D. DeClercq, B. Koenig, S. Schiff and M. Turner assisted in sample collection and laboratory analysis. P. Lyng and A. MacHutchon analyzed DIC and chlorophyll samples at the ELA chemistry laboratory. S. Guildford and M. Turner provided many useful comments on the manuscript.

References

ASOV, Y. 1986. Seasonal patterns of phytoplankton productivity and abundance in nearshore oligotrophic waters of the Levant Basin (Mediterranean). J. Plankton Res. 8: 41–53.

BAKKER, C., P.M.J. HERMAN, AND M. VINK. 1990. Changes in seasonal succession of phytoplankton induced by the storm-surge barrier in the Oosterschelde (S.W. Netherlands). J. Plankton Res. 12: 947–972.

BAYLEY, S.E., D.W. SCHINDLER, K.G. BEATY, B.R. PARKER, AND M.P. STAINTON. 1992. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorous. Can. J. Fish. Aquat. Sci. 49: 584–596.

BOWER, P.M., C.A. KELLY, E.J. FEE, J.A. SHEARER, D.R. DECLERCQ, AND D.W. SCHINDLER. 1987. Simultaneous measurement of primary production by whole-lake and bottle radiocarbon additions. Limnol. Oceanogr. 32: 299–312.

BRUNSKILL, G.J., AND D.W. SCHINDLER. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 139–155.

DEBRUYN, E.R., J.A. SHEARER, AND D.L. FINDLAY. 1982. Phytoplankton primary production, chlorophyll, biomass and suspended carbon in the Experimental Lakes Area—1981 data. Can. Data Rep. Fish. Aquat. Sci. 336: 72 p.

DEBRUYN, E.R., J.A. SHEARER, AND D.L. FINDLAY. 1984. Phytoplankton primary production, chlorophyll, biomass and suspended carbon in the Experimental Lakes Area—1982 data. Can. Data Rep. Fish. Aquat. Sci. 438: 110 p.

DECLERCQ, D.R., AND J.A. SHEARER. 1976. Phytoplankton primary production in the Experimental Lakes Area using an incubator technique—1975 data. Can. Fish. Mar. Serv. Tech. Rep. 647: 127 p.

DECLERCQ, D.R., J.A. SHEARER, S.L. SCHIFF, AND E.J. FEE. 1977. Primary production, respiration, chlorophyll and suspended carbon in the Experimental Lakes Area—1976 data. Can. Fish. Mar. Serv. Data Rep. 32: 94 p.

FEE, E.J. 1973. Modelling primary production in water bodies: A numerical approach that allows vertical inhomogeneities. J. Fish. Res. Board Can. 30: 1469–1473.

FEE, E.J. 1979. A relation between lake morphometry and primary production and its use in interpreting whole-lake eutrophication experiments. Limnol. Oceanogr. 24: 401–416.

FEE, E.J. 1980. Important factors for estimating annual phytoplankton production in the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. 37: 513–522.

FEE, E.J. 1990. Computer programs for calculating in situ phytoplankton photosynthesis. Can. Tech. Rep. Fish. Aquat. Sci. 1740: 27 p.

FEE, E.J., D. HAYWARD, AND J.A. SHEARER. 1982. Annual primary production in lakes of the Experimental Lakes Area, northwestern Ontario: 1976–1980 results. Can. Data Rep. Fish. Aquat. Sci. 327: 33 p.

FEE, E.J., E.U. SCHINDLER, J.A. SHEARER, E.R. DEBRUYN, AND D.R. DECLERCQ. 1991. Light attenuation in the mixed-layer of lakes in the Experimental Lakes Area, 1969–1990 data. Can. Data Rep. Fish. Aquat. Sci. 850: 59 p.

HARRISON, W.G., AND T. PLATT. 1980. Variations in assimilation number of coastal marine phytoplankton: Effects of environmental co-variates. J. Plankton Res. 2: 249–260.

HARRISON, W.G., T. PLATT, AND M.R. LEWIS. 1985. The utility of light-saturation models for estimating marine primary productivity in the field: A comparison with conventional "simulated" in situ methods. Can. J. Fish. Aquat. Sci. 42: 864–872.

HEALEY, F.P., AND L.L. HENDZEL. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Can. J. Fish. Aquat. Sci. 37: 442–453.

JOHNSON, W.E., AND J.R. VALLENTYNE. 1971. Rationale, background, and development of experimental lakes studies in northwestern Ontario. J. Fish. Res. Board Can. 28: 123–128.

LOHRENZ, S.E., D.A. WIESENBURG, C.R. REIN, R.A. ARNONE, C.D. TAYLOR, G.A. KNAUER, AND A.H. KNAP. 1992. A comparison of in situ methods and simulated in situ methods for estimating oceanic primary production. J. Plankton Res. 14: 201–221.

MALLIN, M.A., H.W. PAERL, AND J. RUDEK. 1991. Seasonal phytoplankton composition, productivity and biomass in the Neuse River estuary, North Carolina. Estuarine Coastal Shelf Sci. 32: 609–623.

MALONE, T.C. 1982. Phytoplankton photosynthesis and carbon-specific growth: Light saturated rates in a nutrient-rich environment. Limnol. Oceanogr. 27: 226–235.

MARSHALL, C.T., AND R.H. PETERS. 1989. General patterns in the seasonal development of chlorophyll *a* for temperate lakes. Limnol. Oceanogr. 34: 856–867.

RODHE, W., R.A. VOLLENWEIDER, AND A. NAUWERCK. 1956. The primary production and standing crop of phytoplankton, p. 299–322. *In* A.A. Buzzati-Traverso [ed.] Perspectives in marine biology. University of California press, Berkeley, CA.

SCHINDLER, D.W., K. BEATY, E.J. FEE, D. CRUIKSHANK, E. DEBRUYN, D. FINDLAY, G. LINSEY, J.A. SHEARER, M. STAINTON, AND M.A. TURNER. 1990. Effects of climatic warming on lakes of the western boreal forest. Science (Wash., DC) 250: 967–970.

SCHINDLER, D.W., AND J.E. NIGHSWANDER. 1970. Nutrient supply and primary production in Clear Lake, eastern Ontario. J. Fish. Res. Board Can. 17: 2009–2036.

SHEARER, J.A. 1976. Phytoplankton primary production in the Experimental Lakes Area using an incubator technique—1974 data. Can. Fish. Mar. Serv. Tech. Rep. 616: 142 p.

SHEARER, J.A. 1978. Two devices for obtaining water samples integrated over depth. Can. Fish. Mar. Serv. Tech. Rep. 772: 9 p.

SHEARER, J.A., E.R. DEBRUYN, D.R. DECLERCQ, D.W. SCHINDLER, AND E.J. FEE. 1985. Manual of phytoplankton primary production methodology. Can. Tech. Rep. Fish. Aquat. Sci. 1341: 58 p.

SHEARER, J.A., AND E.J. FEE. 1974. Phytoplankton primary production in the Experimental Lakes Area using an incubator technique—1973 data. Can. Fish. Mar. Serv. Tech. Rep. 474: 110 p.

VOLLENWEIDER, R.A. 1969. A manual on methods for measuring primary production in aquatic environments. IBP Handbook No. 12. Blackwell Scientific Publications, London. 213 p.

WETZEL, R.G. 1983. Limnology. 2nd ed. W.B. Saunders Company, Philadelphia, PA. 767 p.

Phosphorus Budgets and Stoichiometry during the Open-Water Season in Two Unmanipulated Lakes in the Experimental Lakes Area, Northwestern Ontario[1]

P. Campbell

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Campbell, P. 1994. Phosphorus budgets and stoichiometry during the open-water season in two unmanipulated lakes in the Experimental Lakes Area, northwestern Ontario. Can. J. Fish. Aquat. Sci. 51: 2739–2755.

A comparative mass-balance approach is used to describe and quantify phosphorus (P) cycles during the open-water season in two unmanipulated Experimental Lakes Area (ELA) lakes. A bimodal cycle generally prevailed, in which water-column total phosphorus (TP = total dissolved P plus sestonic particulate P) peaked just after ice-out and again late in the summer. Changes in mass of water-column TP were often much larger than corresponding net external inputs. Shifts of P to and from either zooplankton or fish in the water column do not explain the P residuals. Rather, the bottom sediments must have been adding P to the water column. Short-term regeneration of P from the bottom sediments also probably occurs in artificially eutrophied ELA lakes. The mechanism of regeneration is probably biological. Other aspects of P cycling and P stoichiometry are discussed, particularly in relation to nutrient control of population structure and the function of primary and secondary producers.

On a décrit et quantifié les cycles du phosphore (P) durant la saison où les eaux sont libres de glace dans deux lacs non modifiés de la région des lacs expérimentaux en utilisant une méthode comparative d'établissement du bilan massique. De façon générale, on a observé un cycle bimodal dans lequel le phosphore total (PT) de la colonne d'eau (PT = P total dissous + P sestonique particulaire) atteignait un premier maximum juste après la fonte des glaces, puis un deuxième vers la fin de l'été. Les variations de la masse de PT de la colonne d'eau étaient souvent bien plus importantes que les variations des apports externes nets correspondants. On ne peut expliquer les quantités de P résiduelles présentes par les seules absorption et libération de P par le zooplancton ou le poisson dans la colonne d'eau. Il semble plutôt que l'apport de P dans la colonne d'eau provient des sédiments déposés au fond. La régénération à court terme du P attribuable aux sédiments se produit aussi probablement dans les lacs artificiellement eutrophisés de la région des lacs expérimentaux. Le mécanisme de régénération est probablement biologique. Le présent article traite également d'autres aspects du cycle et de la stoechiométrie du P, particulièrement en rapport avec l'influence des éléments nutritifs sur la structure des populations et la fonction des producteurs primaires et secondaires.

Received October 29, 1993
Accepted July 12, 1994
(J12143)

Reçu le 29 octobre 1993
Accepté le 12 juillet 1994

Past research at the Experimental Lakes Area (ELA) that investigated the role of phosphorus (P) as a determinant of plankton community function and structure was conducted on artificially enriched lakes or mesocosms. Phosphorus addition rates were usually orders of magnitude higher than natural external inputs, which could minimize the importance of internal regeneration. The absence of evidence for, and relative unimportance of, sediment feedback or other internal regeneration mechanisms for P may be true of eutrophic systems with large external P inputs (Schindler et al. 1977, 1987; Levine and Schindler 1989, 1992), but may not be true of pristine, oligotrophic Canadian Shield lakes. If the proportions of nutrients derived from internal flows to primary producers were higher in unperturbed lakes than in experimentally enriched systems, then recovery from perturbations might be slower than otherwise expected (Carpenter et al. 1992).

Indirect but significant disruption of the P cycle in oligotrophic lakes may be caused by a variety of other perturbations such as acidification, metal pollution, and global warming, which are being investigated at ELA. To detect, describe, and quantify disruptions to the P regime caused by these perturbations, it is essential to describe the P regimes in natural, unmanipulated ELA lakes. Moreover, the applicability should be established of conclusions drawn from the eutrophication experiments to the interpretation of other experimental perturbations conducted in ELA lakes.

In this paper, a mass-balance approach is used to derive P budgets during the open-water season for two small, dimictic ELA lakes. The seasonal dynamics of water-column P are elucidated and quantified in three ways: (1) relative to external inputs and outputs; (2) in terms of compartment-to-compartment exchanges and pathways; and (3) in terms of spatial and temporal differences in stoichiometry. These analyses provide insight into the importance of internal P flows to plankton community structure and function, particularly in undisturbed, oligotrophic Canadian Shield lakes.

[1]This paper is one of a series done in honor of the 25th anniversary of the Experimental Lakes Area.

Materials and Methods

Study Lakes

Lakes 373 and 442 are located in regrowth boreal forest on the Canadian Shield, 80 km southeast of Kenora, Ont. They are typical of lakes used by ELA researchers for experimental manipulations, and they constitute part of the ELA reference-lake system. Both are also members of the ELA Lake Variation and Climate Change Study flushing series (Campbell 1993b).

The lakes are small, deep, and oligotrophic (Table 1) and they exhibit strong thermal stratification during most of the open-water season (May–October). Both lakes mix completely during fall overturn; however, during the shorter spring circulation, Lake 442 only rarely, if ever, mixes to the bottom. Detailed bathymetric and catchment maps and the hydrometeorology, geology, physiography, and vegetation of the area are described by McCullough and Campbell (1993). Lake 373 is a headwater lake, and has a theoretical water-renewal time of 25 yr (calculated over the period 1987–90). Second-order Lake 442 has a smaller volume and larger catchment than Lake 373, and has a flushing time of 11 yr. Lake trout (*Salvelinus namaycush*) is the top predator in both lakes. Lake 442 is probably the smallest lake in the ELA to support a viable lake trout population (K. Mills, Department of Fisheries and Oceans, Winnipeg, MB, personal communication).

Field Measurements, Sampling, and Laboratory Analysis

Lake levels and flows

Lake water levels were recorded biweekly throughout the open-water season, using permanent, 1-m staff gauges read to the nearest millimetre (Cruikshank et al. 1993; D. Cruikshank, Department of Fisheries and Oceans, Winnipeg, MB, unpublished data). The outflow from Lake 373 was monitored continuously with a Leopold Stevens model A-71 water level recorder installed over the stilling pond above a V-notch weir located ≈175 m downstream of the lake. Discharge was obtained by regression of the logarithms of discharge and head based on occasional manual metering that covered the full range of hydrological conditions. Mean daily discharges from Lake 373 for 1991 and 1992 were obtained from K. Beaty and M. Lyng (Department of Fisheries and Oceans, Winnipeg, MB, unpublished data). Outflow from Lake 442 was not measured directly during the course of this study.

Chemistry samples

Inflowing and outflowing streams were sampled once every 2 wk during the open-water season, and at least twice before ice-out. Stream water samples were collected by hand in 500-mL polyethylene bottles. Lakes 373 and 442 were sampled every 4 wk at 1-m intervals in a vertical profile, by the same operator, using a Masterflex J-757Q peristaltic pump and Tygon tubing. Lakes like 373 and 442 exhibit marked vertical gradients in nutrient distribution, so sampling at 1-m intervals provided for good spatial resolution. Moreover, high numbers of individual samples (18–20) from the water column of these dilute lakes improved the precision on calculations of constituent masses in the water column (Campbell 1993a). This is of particular importance in lakes where elements such as P are sometimes at or near the limits of detection of standard analytical methods routinely employed at the ELA.

TABLE 1. Morphometry of lakes 373 and 442. A_D = drainage area above lake outlet and including lake surface area; A_L = lake surface area; Z_m = maximum depth; z = mean depth; V = whole-lake volume; L = length of shoreline; and F_L = shoreline development (data from McCullough and Campbell 1993).

Lake	A_D (ha)	A_L (ha)	Z_m (m)	z (m)	V ($m^3 \times 10^5$)	L (m)	F_L[a]
373	80.6	27.3	20.8	11.0	30.09	2790	1.51
442	161.0	16.0	17.8	9.0	14.40	2470	1.74

[a] $F_L = L/2\pi A_L$ (Hutchinson 1957).

Precipitation was collected from May to October in a bulk sampler (Linsey et al. 1987) located on an island in Lake 240, ≈12 and 15 km from Lakes 373 and 442, respectively. Chemical analyses were performed either when precipitation events (single or accumulated) exceeded 2 mm or at 24-h intervals during continuous rainfall.

Sample processing protocols and analytical procedures were described by Stainton et al. (1977). Raw water samples were kept cool and stored in the dark prior to processing. Filtrations were done within 24 h from the time of collection. Particles were collected on preignited Whatman 4.25-cm GF/C filters, which were dried or desiccated overnight. Filters were stored frozen until analysis. Filtration aliquots were normally 100 mL; the filtrate was saved for determinations of dissolved constituents.

Chlorophyll *a* was measured using the gross fluorescence method (Stainton et al. 1977), except that the extraction solvent was 95% methanol. Particulate phosphorus (PP) was determined spectrophotometrically as orthophosphate (molybdenum blue reaction) following filter ignition and extraction with dilute hydrochloric acid. Particulate carbon (PC) was measured by combusting the filter in an oxygen–helium atmosphere, oxidizing the organics to carbon dioxide (CO_2), and analysis by thermal conductance detector (Carlo Erba Model 1102 CHN analyzer). The molybdenum-blue spectrophotometric technique for orthophosphate was also used to analyze for total dissolved phosphorus (TDP) after digestion of organic compounds by acidification and conversion to phosphates by ultraviolet photooxidation. Total dissolved inorganic carbon (DIC) was measured using infrared detection of CO_2 sparged from acidified samples. Total dissolved organic carbon (DOC) was measured by infrared detection of CO_2 on a separate subsample after rapid persulphate digestion.

Primary production

Samples for determining rates of algal photosynthesis were collected with the integrating-bottle sampler described by Shearer (1978). Samples were taken biweekly, May through August, and once per month in September and October. In 1990 and 1991, primary-production samples were collected only from the epilimnion (lake surface to the depth at which temperature change first exceeded $1°C \cdot m^{-1}$; Cruikshank et al. 1993; D. Cruikshank, unpublished data). In 1992, a second integrated sample was also collected from the remainder of the photic zone (i.e., from the bottom of the epilimnion to the depth at which photometrically determined light transmittance was 1% of that measured in air just above the lake surface; Cruikshank et al. 1993; D. Cruikshank, unpublished data).

Sample processing commenced within 4 h of collection. The ^{14}C method used for estimating rates of phytoplankton

photosynthesis followed Shearer et al. (1985) and Hendzel et al. (1995). Samples were incubated at in situ temperatures (±1°C) for 3 h at five different light intensities covering the in situ range measured photometrically (Cruikshank et al. 1993; D. Cruikshank, unpublished data). Following incubation, unassimilated radioactive C was removed by bubbling, scintillation fluor was added, and counting was done within a few hours on a Beckman LS-8000 liquid scintillation counter. Procedures used to calculate photosynthesis rates are outlined in Shearer et al. (1985).

Zooplankton

Zooplankton was collected biweekly from seven pelagic and eight littoral stations in each of Lake 373 and Lake 442 (see Salki 1993 for details). Littoral stations were located on the 3-m contour interval; pelagic stations were selected to give balanced coverage of the deep zone. The water column was sampled to within 0.25–0.5 m of the bottom. Samples were poured through 72-μm-mesh nets. Littoral samples were composited in a single net. Pelagic 1990 samples from Lake 442 were composited into two separate nets: 0–5 m and 5 m – bottom. In 1991 and 1992, three pelagic composites were taken: 0–5 m, 5–9 m, and 9 m – bottom for Lake 442, and 0–6 m, 6–12 m, and 12 m – bottom for Lake 373. Zooplankters were preserved in 5% formalin.

Counting and identification procedures were described by Salki (1993). Samples were settled and concentrated to 40 mL. Subsamples (1 mL) were identified and enumerated using a 63× compound microscope. All specimens except cyclopoid and diaptomid nauplii were identified to species. Total abundance estimates with errors <7% were achieved for the most common species by counting a minimum of 200 individuals. For larger, less abundant species, specimens were enumerated under a 12× dissecting microscope and the entire 40-mL sample was examined to minimize counting errors. Numbers of specimens per unit volume were converted to biomass from specimen lengths and conversion formulae as reported by Salki (1992).

Computations

Water budgets

Water budgets for the Lake 373 and Lake 442 catchments were constructed over time intervals corresponding exactly with lake sampling intervals. For each time interval, total depth of precipitation (P_t) was obtained by summing daily precipitation values recorded at the ELA meteorological station (K. Beaty and M. Lyng, unpublished data). The corresponding volume of precipitation that fell on a lake's surface (P_L) was derived by multiplying total accumulated depth of precipitation by the lake surface area (A_L). Similarly, the volume of precipitation delivered to the remainder of the catchment (P_T) was calculated by multiplying precipitation input by terrestrial catchment area (A_T). For Lake 442, A_T included the surface area of upstream Lake 438 as well as the terrestrial catchment. Changes in lake water storage during any interval were derived by subtracting the staff gauge height recorded at the end of the interval from that recorded at its start. The difference in height was multiplied by A_L to obtain change in lake storage volume (S_L).

Daily outlet discharge measurements for Lake 373 (K. Beaty and M. Lyng, unpublished data) were summed to obtain total outlet discharge for the sampling interval (Q_o). Total terrestrial runoff into the lake (R_T) was derived by extrapolating from the northwestern subcatchment of the Lake 239 index catchment (Schindler et al. 1976). For each 4-wk time interval considered here, specific runoff coefficients were derived for the northwestern subcatchment of Lake 239 by dividing total stream discharge from the subcatchment (K. Beaty and M. Lyng, unpublished data) by the total amount of precipitation entering it. Northwestern subcatchment runoff coefficients were applied to the precipitation entering the terrestrial catchment of Lake 373 to obtain R_T. R_T was subsequently proportioned among specific subcatchments as a direct function of subcatchment area relative to total catchment area (refer to McCullough and Campbell 1993 for catchment maps and areas). Factors applied were: southwestern subcatchment runoff, $R_{SW} = 0.081R_T$; southeastern subcatchment runoff, $R_{SE} = 0.214\ R_T$; and runoff from undefined catchment area, $R_U = 0.705\ R_T$. Water loss by evaporation from the lake surface (E_L) was estimated by difference between hydrological inputs and outputs, where $E_L = P_L + R_T - S_L - Q_o$. As a check, pan evaporation coefficients were calculated using derived lake evaporation estimates and class A pan evaporation measured at the ELA (K. Beaty and M. Lyng, unpublished data). Pan coefficients ranged from 0.25 in spring to 1.5 in fall. This trend from smaller to larger coefficients as the open-water season progressed was particularly obvious in the warmer, drier years, and agreed with observations on Lake 239 (Newbury and Beaty 1980). The pan coefficients calculated for Lake 373 all fell within the range of those reported for Lake 239 for the period 1972–76 (0.32 ± 0.23 in May to 1.09 ± 0.97 in October).

Hydrological inputs to Lake 442 via terrestrial runoff were also estimated by extrapolation from the Lake 239 catchment (K. Beaty and M. Lyng, unpublished data). Runoff coefficients from the northwestern subcatchment (A_d = 56.4 ha) were applied to precipitation inputs to the undefined catchment area directly adjacent to Lake 442 (A_d = 35.8 ha). Runoff coefficients derived for the eastern subcatchment of Lake 239 (A_d = 170.3 ha) were applied to precipitation entering the northern subcatchment of Lake 442 (A_d = 109.2 ha). During the 3-yr period of this study, monthly runoff coefficients for the northwestern and eastern subcatchments of Lake 239 were highly variable, ranging from practically zero (both subcatchments, late summer 1990 and 1991) to 2.12 for the northwestern subcatchment in April 1992. Total terrestrial runoff to Lake 442 was calculated by summing subcatchment runoffs: $R_T = R_N + R_U$, where R_N is runoff from the northern subcatchment and R_U is undefined runoff. In 1991 and 1992, lake evaporation (E_L) was estimated by extrapolating directly, on an areal basis, from Lake 373. For June, July, and August of 1990, pan coefficients derived for the same months in 1991 were applied to class A pan evaporation measured at the ELA (K. Beaty and M. Lyng, unpublished data) to derive lake evaporation; discharge via the outlet (Q_o) was then estimated by the equation $Q_o = P_L + R_T - E_L - S_L$. In September and October of 1990, outlet discharge was zero; for these two months, lake evaporation (E_L) was estimated in the same way as for Lake 373 (i.e., inputs minus outputs). Groundwater inflows and outflows from both Lake 442 and Lake 373, which lie in bedrock-controlled basins, were assumed to be negligible (Schindler et al. 1976).

Phosphorus budgets

Inputs of P by precipitation falling directly on the lake surface were estimated for each rainfall event. P loading

TABLE 2. Open-water season (May 1 – October 31) precipitation and mean daily air temperatures at the Experimental Lakes Area. Data from Beaty and Lyng (1989) and K. Beaty and M. Lyng (Department of Fisheries and Oceans, Winnipeg, MB, unpublished data).

	Precipitation (mm)	Air temperature (°C)
1970–1989	464.6	13.6
1990	373.7	13.6
1991	555.6	14.3
1992	624.7	12.0

rates were calculated by multiplying precipitation volume by concentration of P measured in that precipitation. Single-event loadings were then summed over the time interval of interest to obtain total inputs of TDP and PP. Total phosphorus (TP) input directly to the lake surface by precipitation (P_P) was calculated by summing inputs of TDP and PP.

Total dissolved P and PP concentrations in inflowing streams (southwestern inlet, Lake 373; southeastern inlet, Lake 373; and northern inlet Lake 442) were measured biweekly. The two P determinations during a 4-wk period were averaged when streams were flowing; the average was multiplied by the corresponding flow to derive subcatchment P loading rates. For undefined runoff in the Lake 373 watershed, P concentrations were the average of all those measured in both the southeastern inlet and the southwestern inlet during the appropriate period. This same average derived from Lake 373 subcatchments was also applied to undefined runoff in the Lake 442 basin. Total P inputs via terrestrial runoff (R_P) were obtained by summing inputs from all subcatchments, both defined and undefined. Total P input from external sources was calculated as: $I_P = P_P + R_P$.

Concentrations of TDP and PP in outflowing streams were also normally measured biweekly. As with stream inflows, outflow P concentrations during a 4-wk period were averaged and then applied against the corresponding hydrological outflow to obtain the P removal rate. Total dissolved P and PP outputs were summed to obtain TP exiting through the outlet (O_P). Net input of P from external sources was calculated as: $P_{net} = I_P - O_P$.

Water column P masses (dissolved and sestonic) were calculated for depth intervals of 1 m using TDP and PP concentrations derived from the profile samples. Lake volumes, in 1-m slices, were taken from McCullough and Campbell (1993) and multiplied by the corresponding P concentration to obtain the mass of P in the stratum. Phosphorus masses for three depth zones roughly corresponding to the midsummer epilimnion, the metalimnion (i.e., photic zone minus the epilimnion), and the hypolimnion were derived by summing metre-interval masses. For Lake 442, the midsummer epilimnion was defined as lying between 0 and 4 m; the metalimnion from 4 to 10 m; and the hypolimnion from 10 m to the bottom (≈18 m). For Lake 373, the same depth zones were taken to be 0–6 m, 6–14 m, and 14–20.5 m, respectively. Whole-lake P masses (L_P) were calculated by summing all metre-interval P masses.

A residual term (X_P) expressed gains or losses in water-column P (dissolved and/or sestonic) unaccounted for by measured inputs or outputs. Over the course of a sampling interval, the residual term was calculated as: $X_P = \Delta L_P - P_{net}$. A positive value of X_P implied a gain in water-column P from internal source(s). A negative value of X_P implied losses from solution and/or seston that exceeded external removal via the outflow.

TABLE 3. Relative contributions (%) of precipitation (P_L), runoff (R_T), storage (S_L), evaporation (E_L), and outlet discharge (Q_o) to hydrological inputs and outputs of Lakes 442 and 373 during the open-water season.

	P_L	R_T	S_L	E_L	Q_o
Lake 442					
1990 (June 6 – Oct. 3)	39	44	17	48	52
1991 (May 8 – Oct. 22)	30	54	16	28	72
1992 (May 13 – Nov. 2)	21	78	1	13	87
Lake 373					
1991 (May 22 – Oct. 8)	71	26	3	60	40
1992 (May 20 – Nov. 2)	53	37	10	32	68

Results

Hydrometeorology

The three study years covered a wide range of weather conditions. The open-water season of 1990, the last in a series of five consecutive drought years, was much drier than average (Table 2). In 1991, however, precipitation was 20% above normal for the May–October period. The summer of 1992 was among the wettest (34% above normal) and by far the coolest during the historical record (July was 4.2°C below normal). As a result, watershed yields ranged widely among the three study years. Water inputs from the terrestrial catchments of Lake 373 and Lake 442 were essentially zero in some later summer months in 1990 and 1991. For the May–October period, highest yields from the terrestrial catchment (up to 90%) occurred in May and June; in average or wet years, catchment yields were also relatively high in the fall (≈50–60% in some months). In wetter years, the relative contribution of catchment inputs and outputs increased (Table 3).

Hydrological inputs and outputs at the lake surface were of primary importance for headwater Lake 373 during the open-water season (Table 3). Precipitation falling directly on the surface provided 71% (1991) and 53% (1992) of the water entering Lake 373 during the open-water periods. In 1991, 60% of the water lost was by evaporation from the lake's surface; however, in very damp and cool 1992, evaporation accounted for only 32% of water loss. For second-order Lake 442, watershed inflows and outflows were larger than lake-surface phenomena. In wet 1992, nearly 80% of inflow was runoff from the terrestrial catchment, which was almost double the proportion attributable to the terrestrial catchment in dry 1990. The 67% increase in precipitation from 1990–92 caused terrestrial runoff to increase by more than five times. Drawdown of water stored during early spring peak flows was also a significant component in both 1990 and 1991, accounting for 16–17% of the Lake 442 May–October water budget. Precipitation falling directly on the lake surface accounted for 21–39% of the total water entering the lake. Water loss by evaporation from Lake 442 ranged from 13% in 1992 to 48% in 1990.

TABLE 4. Contributions of precipitation (P_p), runoff (R_p), and flow via the outlet (O_p) to inputs and outputs of total phosphorus (T_p) for Lakes 442 and 373 during the open-water season. External TP inputs: $I_p = P_p + R_p$.

	(P_p/I_p) 100 (%)	(R_p/I_p) 100 (%)	I_p (g)	O_p (g)	P_{RET} (%)[a]
		Lake 442			
1990 (June 6 – Oct. 23)	64.4	35.6	1568	555	64.6
1991 (May 8 – Oct. 22)	46.4	53.6	3454	1975	42.8
1992 (May 13 – Nov. 2)	38.9	61.1	8685	3494	59.8
		Lake 373			
1991 (May 22 – Oct. 8)	72.0	28.0	2331	456	80.4
1992 (May 20 – Nov. 2)	73.0	27.0	6438	1168	81.9

[a]P_{RET} = percent lake retention of phosphorus = $100(I_p - O_p/I_p)$.

TABLE 5. Loading rates of total phosphorus (TP) to Lakes 442 and 373 during the open-water season. I_p = external TP inputs; O_p = loss of P through the outflow.

	Gross = I_p			Net = $I_p - O_p$		
	g	$mg \cdot d^{-1}$	$\mu g \cdot d^{-1} \cdot m^{-2}$	g	$mg \cdot d^{-1}$	$\mu g \cdot d^{-1} \cdot m^{-2}$
			Lake 442			
1990 (June 6 – Oct. 23)	1568	11 200	70	1013	7 240	45
1991 (May 8 – Oct. 22)	3454	20 700	128	1479	8 860	55
1992 (May 13 – Nov. 2)	8685	50 200	314	5191	30 000	188
			Lake 373			
1991 (May 22 – Oct. 8)	2331	16 800	61	1875	13 500	49
1992 (May 20 – Nov. 2)	6438	38 800	142	5270	31 700	116

Phosphorus Budgets and Water Column Cycles

The relative contributions of precipitation and runoff to P loading in Lake 442 and Lake 373 (Table 4) were tied closely to hydrological inputs. In 1990, precipitation falling on the surface accounted for nearly 65% of the P input to Lake 442 during the June–October period. In wet years, the P contributed by precipitation falling directly on the surface of Lake 442 tended to diminish relative to runoff; in 1992, this source constituted <40% of the total. For headwater Lake 373, however, precipitation falling on the surface was the dominant component in 1991 and 1992, accounting for >70% of P input from external sources. Phosphorus retention by unfertilized ELA lakes is a direct function of hydrologic flushing time, which is illustrated by the lake-to-lake differences in P retention presented here. Phosphorus retention by Lake 373, the slower flushing system, was ≈80%, whereas in Lake 442 (water renewal time is approximately half that of Lake 373) open-water season P-retention rates were ≈50%. As gross areal-loading rates of P increased, retention rates decreased. As a result, lake-to-lake differences in net areal loading rates of P tended to be smaller than expected from lake-to-lake differences in gross areal loading rates (Table 5). For example, in 1991, the gross areal loading rate of P to Lake 442 during the open-water season was 128 $\mu g \cdot d^{-1} \cdot m^{-2}$; for Lake 373, the rate was 61 $\mu g\ P \cdot d^{-1} \cdot m^{-2}$; i.e., the gross P-loading rate to Lake 442 was 110% more than to Lake 373. However, differences in the corresponding net areal loading rates (adjusting I_p for O_p) were only 12%. Net areal-loading rates of P to Lake 442 and Lake 373 during the open-water season were very low, ranging from about 0.05–0.2 $mg \cdot d^{-1} \cdot m^{-2}$ (Table 5). This compares with ≈3 $mg \cdot d^{-1} \cdot m^{-2}$ for artificially eutrophied Lake 227 (Schindler et al. 1987). Annual P-retention rates for headwater reference Lake 239 during the early 1970s ranged from 67–79% (Schindler et al. 1976).

Total P contained in the water column varied considerably through the open-water season (Fig. 1). Whole-lake P mass changed by as much as 47% in a single month. A general pattern in seasonal changes of whole-lake P masses can be discerned from Fig. 1: (1) a large addition of P to the water column at time of ice-out; (2) a period of rapid decline in water-column P during a clear-water phase in late May and June; (3) a rise in P by late summer to near the maximum observed just after ice-out; and (4) a fall decline to the low levels of P observed during late spring.

Figures 1–3 illustrate locations where major changes in water-column P content occurred. The first increase in water-column P observed at ice-out was visible mainly in the metalimnion and epilimnion, and was associated mostly with the sestonic fraction (Fig. 3). The subsequent decrease during the late-spring, clear-water phase also mainly occurred in the epilimnion and metalimnion; P in solution (Fig. 2)

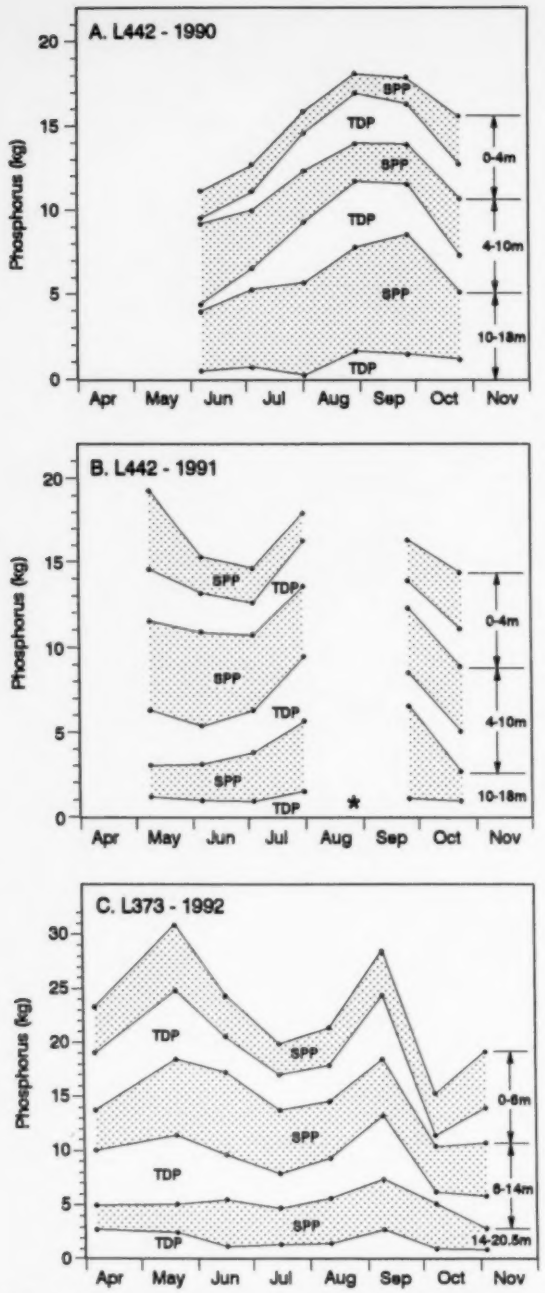


FIG. 1. Masses of phosphorus (P) in the water columns of Lakes 442 and 373. (A) Lake 442, 1990. (B) Lake 442, 1991. (C) Lake 373, 1992. The water column has been divided in three strata that roughly coincide with (1) midsummer epilimnion, (2) the remainder of the photic zone (≈ metalimnion), and (3) the hypolimnion. In Lake 442, these three strata were located at 0–4 m, 4–10 m, and 10 m – bottom, respectively. For Lake 373, the depths were 0–6 m, 6–14 m, and 14 m – bottom. Quantities shown are cumulative; the top line, therefore, represents total lake P. TDP = total dissolved phosphorus; SPP = sestonic particulate phosphorus. *Samples collected Aug. 28, 1991, for TDP analyses were spoiled.

and seston PP (SPP) (Fig. 3) declined. The summer recharge of P, which tended to peak in September, occurred mainly in the hypolimnion and epilimnion. The increase in hypolimnetic P over the summer was large and almost totally particulate. For Lake 442, PP not only built up in the hypolimnion over the course of the summer but a simultaneous breakdown of the vertical concentration gradient occurred, which suggested hypolimnetic mixing of sestonic P. Over the summer, large amounts of P were added to the epilimnion but, in contrast to the hypolimnion, it was all dissolved P. During the summer replenishment of water-column P, the mass of TP in the metalimnion was stable; TDP increased, but SPP decreased. The large decline in water-column P during fall overturn occurred mainly in hypolimnetic SPP. Particulate P may have increased during maximum circulation, just before freeze-up, in the former epilimnion and metalimnion.

Month-to-month changes in water-column TP were often many times larger than could be accounted for by external inputs–outputs (Fig. 4; Table 6). The result often was a large positive or negative residual term (X_P), which implied significant internal regeneration or removal–storage (see below).

Phosphorus Stoichiometry

Phosphorus content of the seston increased with depth in both Lake 373 and Lake 442 (Table 7; Fig. 5). Suspended particles in the hypolimnion were, on average, two to three times richer in P than epilimnetic seston. At commencement of the open-water season, the sestonic C/P ratio (sestonic PC [SPC]/SPP) was relatively constant throughout the water column and P content was high. Phosphorus in the hypolimnetic seston remained high and varied little throughout the open-water season. However, as the summer progressed, a major divergence occurred in the surface waters, particularly in the epilimnion but also in the metalimnion. In both strata, SPP became progressively depleted relative to SPC; maximum depletion was generally August–September (Fig. 5). During fall overturn, SPP/SPC ratios in the former epilimnion and metalimnion increased, returning to the relatively P-rich situation of early spring. Sestonic P/C ratios in Lake 442 appeared to increase between 1990 and 1992; little difference was apparent in Lake 373 between 1991 and 1992 (Table 7). Overall, suspended particles in Lake 442 were somewhat richer in P than those in Lake 373, perhaps because Lake 442 had a higher proportion of allochthonous particles, concomitant with a water renewal rate higher than that of Lake 373 (Hecky et al. 1993). The majority of sestonic C/P determinations in this study were considerably higher than the Redfield ratio of 41 (Fig. 5). Carbon/P ratios were as low as the Redfield ratio on only three occasions (once in Lake 442 and twice in Lake 373), and only in very deep waters. Schindler and Fee (1974) hypothesized that nutrient consumption in the hypolimnion by bacteria, instead of algae, was responsible for decreasing C:N:P ratios in seston with depth. Hecky et al. (1993) suggested that selective gaseous loss of C from particles by respiration prior to burial was the simplest interpretation of C/P ratios lower in sediment particles than in epilimnetic seston (see below).

Enrichment of the bottom waters of Lakes 442 and 373 with dissolved P relative to dissolved C species also apparently occurred. However, the difference in dissolved P/C ratios between surface waters and bottom waters was not nearly as pronounced as for the seston, and no temporal

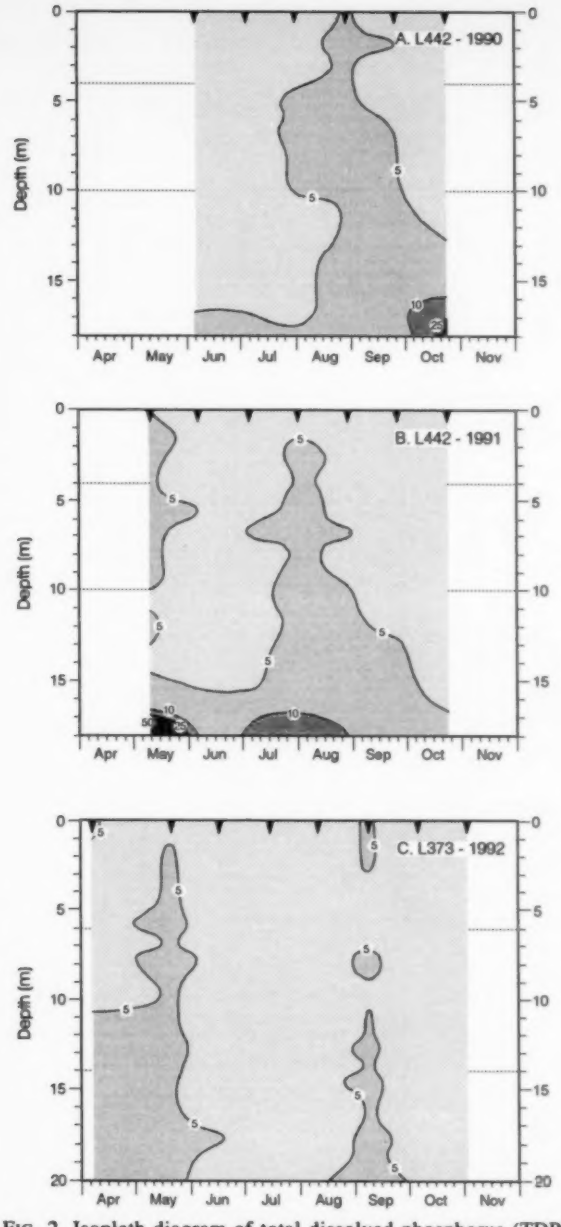


FIG. 2. Isopleth diagram of total dissolved phosphorus (TDP; $\mu g \cdot L^{-1}$) concentrations during the open-water season. (A) Lake 442, 1990. (B) Lake 442, 1991. (C) Lake 373, 1992. Lake 373 was ice covered during the first sampling interval, April 6 – May 19.

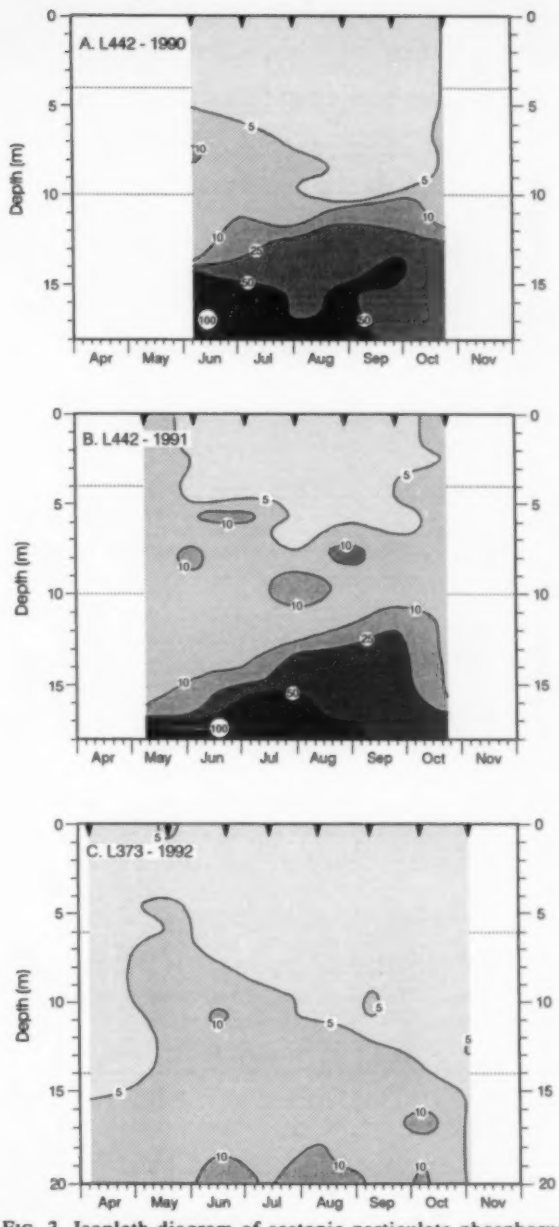


FIG. 3. Isopleth diagram of sestonic particulate phosphorus (SPP; $\mu g \cdot L^{-1}$) concentrations during the open-water season. (A) Lake 442, 1990. (B) Lake 442, 1991. (C) Lake 373, 1992. Lake 373 was ice covered during the first sampling interval, April 6 – May 19.

trends were obvious for dissolved material. Rather, enrichment of the hypolimnion in dissolved P appeared to be largely a function of occasional, episodic injection events such as were particularly obvious in the anoxic bottom waters of Lake 442 (Fig. 2A and 2B). In only two of five lake-years did an obvious difference exist in TDP/DIC ratios between deep waters and the surface: Lake 442 in 1991 and 1992 (Table 7). The apparent hypolimnetic enrichment in dissolved P in 1991 was mainly a function of a single event in May (Fig. 2B). In 1992, the difference was a function of extremely high hypolimnetic TDP concentrations recorded in April and May. TDP/DIC ratios were higher than P/C in suspended particles; the largest difference occurred in the epilimnion where TDP/DIC was approximately three times higher than SPP/SPC.

It is informative to compare chlorophyll *a* / SPP plots (Fig. 6) with those of SPC/SPP (Fig. 5). The hypolimnetic

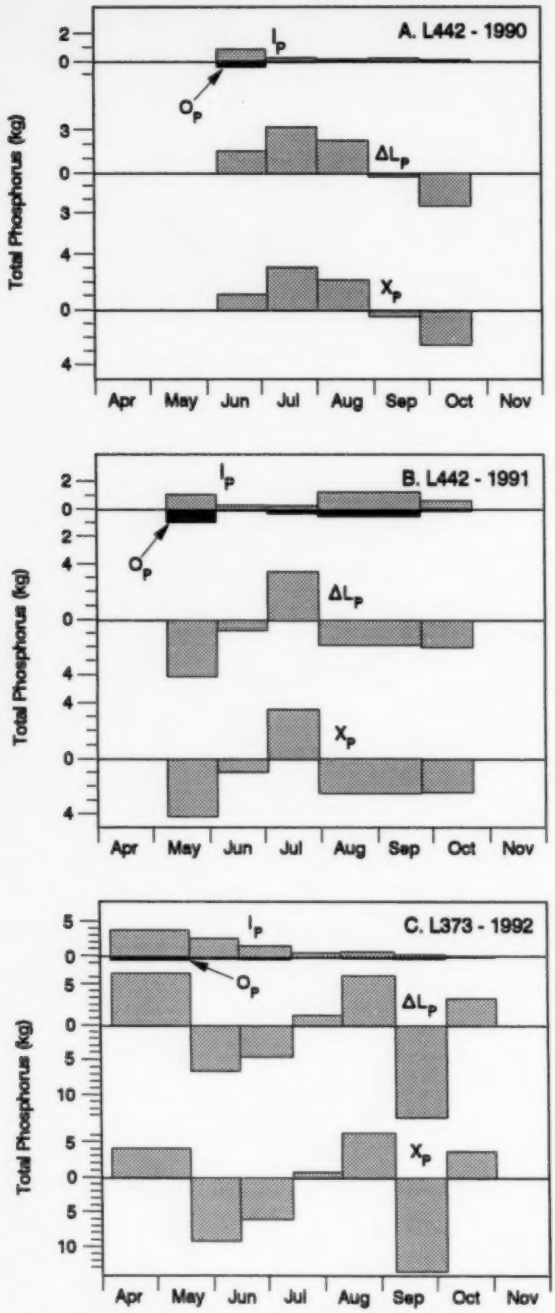


FIG. 4. Total phosphorus (TP) budgets at 4-wk intervals for Lakes 442 and 373 during the open-water season. (A) Lake 442, 1990. (B) Lake 442, 1991. (C) Lake 373, 1992. Lake 373 was ice covered during the first sampling interval, April 6 – May 19. I_P = total input of P from external sources; O_P = P removal via the outlet stream; ΔL_P = change in total mass of P (dissolved + sestonic) in the water column; and, $X_P = \Delta L_P - (P_{net})$, a residual term.

TABLE 6. Budgets for total phosphorus (TP) in Lakes 442 and 373. The budgets were constructed over 4-wk intervals that corresponded exactly with lake chemistry sampling schedules. See text for computational procedures and assumptions. P_{net} = net input of P from external sources; ΔL_P = change in mass of whole-lake, water-column P (dissolved + sestonic) during a sampling interval; $X_P = \Delta L_P - P_{net}$, i.e., a residual term equal to the portion of water-column P gained or lost, not accounted for by external input–output terms. $\Delta L_P \cdot P_{net}^{-1}$ is an expression of the change in dissolved plus sestonic water-column P content relative to corresponding net external input of TP.

	P_{net} (g)	ΔL_P (g)	X_P (g)	$\Delta L_P \cdot P_{net}^{-1}$
		Lake 442, 1990		
June 6 – July 3	434	1 564	1 130	3.6
July 4 – July 31	150	3 169	3 019	21.1
Aug. 1 – Aug. 28	127	2 254	2 127	17.7
Aug. 29 – Sept. 25	201	−219	−420	−1.1
Sept. 26 – Oct. 23	101	−2 305	−2 406	−22.8
June 6 – Oct. 23	1013	4 463	3 450	4.4
		Lake 442, 1991		
May 8 – June 4	145	−3 992	−4 137	−27.5
June 5 – July 2	224	−708	−932	−3.2
July 3 – July 30	−21	3 456	3 477	∞
July 31 – Sept. 24[a]	703	−1 752	−2 455	−2.5
Sept. 25 – Oct. 22	428	−1 937	−2 365	−4.5
May 8 – Oct. 22	1479	−4 933	−6 412	−3.3
		Lake 442, 1992		
Apr 6 – May 12	1108	5 991	4 883	5.4
May 13 – June 1	1011	−1 200	−2 211	−1.2
June 2 – July 28[b]	2620	−1 165	−3 785	−0.4
July 29 – Aug. 23	543	569	26	1.0
Aug. 24 – Sept. 20	878	−974	−1 852	−1.1
Sept. 21 – Oct. 20	143	−786	−929	−5.5
Oct. 21 – Nov. 2	−4	−3 044	−3 040	761
Apr 6 – Nov. 2	6299	−609	−6 908	−0.1
		Lake 373, 1991		
May 22 – June 18	610	−2 866	−3 476	−4.7
June 19 – July 16	186	2 378	2 192	12.8
July 17 – Aug. 13	230	840	610	3.7
Aug. 14 – Sept. 10	260	−6 349	−6 609	−24.4
Sept. 11 – Oct. 8	589	344	−245	0.6
May 22 – Oct. 8	1875	−5 653	−7 528	−3.0
		Lake 373, 1992		
Apr 6 – May 19	3324	7 599	4 275	2.3
May 20 – June 15	2479	−6 517	−8 996	−2.6
June 16 – July 14	1350	−4 526	−5 876	−3.4
July 15 – Aug. 10	567	1 460	893	2.6
Aug. 11 – Sept. 8	693	7 211	6 518	10.4
Sept. 9 −Oct. 6	104	−13 265	−13 369	−127.5
Oct. 7 – Nov. 2	77	3 905	3 828	50.7
Apr 6 – Nov. 2	8594	−4 133	−12 727	−0.5

[a]Time interval is twice normal because of a problem with TDP analyses on Aug. 28.

[b]Time interval is twice normal because of a problem with SPP analyses on June 30.

TABLE 7. Comparison of sestonic particulate phosphorus / sestonic particulate carbon ratio (SPP/SPC) with P/C release ratio (total dissolved phosphorus / dissolved inorganic carbon [TDP/DIC]) in Lakes 442 and 373 during the open-water season. Ratios are expressed as μg P·mg C^{-1}.

	1990		1991		1992	
Depth (m)	SPP/SPC	TDP/DIC	SPP/SPC	TDP/DIC	SPP/SPC	TDP/DIC
			Lake 442			
0–4	5.2	18.8	6.9	24.8	7.9	22.6
4–10	8.0	19.2	9.0	23.7	11.0	19.6
10–18	15.7	17.2	17.3	29.7	19.0	40.7
			Lake 373			
0–6	—	—	6.5	15.3	6.7	18.0
6–14	—	—	8.4	17.5	9.0	18.7
14–20.5	—	—	13.3	17.5	12.9	19.3

chlorophyll *a* / SPP ratio was normally much lower than in the epilimnion or metalimnion, which paralleled the divergence pattern for SPC/SPP, except for one notable difference. Occasionally, major episodic excursions occurred when, over a short time interval, deep-water chlorophyll increased dramatically (Fig. 7; see also Fee et al. 1977; Fee 1978). The hypolimnetic chlorophyll *a* / SPP ratios that resulted were many times higher than those in shallower zones (Fig. 6C). Moreover, unlike SPC/SPP, no uninterrupted, season-long separation of epilimnetic from metalimnetic chlorophyll *a* / SPP ratios occurred. Rather, there was much overlap and, for large portions of the open-water season, chlorophyll *a* / SPP in the metalimnion was considerably higher than in the epilimnion. This was in contrast to SPC/SPP where, once having diverged following spring overturn, the epilimnion seston maintained C/P ratios higher than in the metalimnion. These observations suggested that P enrichment of seston in the bottom waters was not simply an artifact of detrital respiration processes, but it may have been at least partly a function of deep-water algae and/or bacteria actively absorbing and storing P required for autotrophic or heterotrophic metabolic processes.

Discussion

Dissolved and Particulate Phosphorus

Primary production results from this study implied a supply of P to the surface waters by unknown sources and/or significant recycling within the water column. Photosynthetic uptake of P in Lake 442 and Lake 373 ranged from 3 to 10 times the external supply rate from precipitation and runoff (Table 8). On an areal basis, the difference between photosynthetic requirements and gross supply by external sources ranged from 470 to 890 μg $P \cdot d^{-1} \cdot m^{-2}$. These estimates of P recycling in the euphotic zone and/or inputs from unmeasured sources are probably conservative because removal from the water column by sedimentation or through the outlet was not considered, and it was unreasonable to assume that all P supplied to the lakes by runoff or precipitation was in a form utilizable by photosynthetic algae. Schindler and Fee (1974) and Levine and Schindler (1980) also concluded that P supplied from external sources was insufficient to support algal photosynthesis in ELA lakes. These authors determined that phosphate (PO_4^{2-})-P was turned over thousands of times prior to removal by sedimentation.

In addition to rapid metabolic recycling of P through the primary producers, the current study also demonstrated short-term accumulations and depletions of standing stocks of water-column P (Table 6; Fig. 1 and 4) that could not be explained simply as a function of supply from external sources and/or removal through the outlet. The biphasic pattern observed over the open-water season, which included a buildup of TP culminating in maximum water-column content at the end of summer (Fig. 1), was similar to that reported for small (20 ha), subalpine Castle Lake, California (Elser and George 1993).

Emerson and Hesslein (1973), Schindler et al. (1975, 1977), and Schindler (1975) showed that physical or chemical processes were ineffective in regenerating P from ELA lake sediments, whether conditions were anoxic or oxic, i.e., the classical concept of oxygen (O_2) control was not in evidence. Levine and Schindler (1980) concluded that PO_4^{2-} concentrations were biotically rather than abiotically regulated in ELA lakes. Elsewhere, Caraco et al. (1991) showed that sulphate (SO_4^{2-}) concentration was more important than O_2 in explaining differences in sediment-P release rates; however, a large residual (35%) still remained in their study of 23 lakes. In Lake 442 and Lake 373, TDP/DIC release ratios of approximately 7 mmol $P \cdot mol^{-1}$ C were within the range 3–10 expected as a function of decomposing, freshly sedimented organic matter and typical of most aquatic systems (Caraco et al. 1991). Usually, little difference existed in TDP/DIC release ratios among depth zones (Table 7), which suggested that O_2 or SO_4^{2-} were not generally the major controllers of sediment P release, even in Lake 442 which develops an anoxic hypolimnion as the summer progresses.

Phosphorus that has disappeared or appeared in the water column in quantities exceeding expectations has, typically, been attributed to sedimentation or sediment regeneration. Phosphorus removal by sedimentation in artificially eutrophied ELA systems was demonstrated repeatedly, by mass-balance calculations in which sedimentation was estimated as the difference between external loading and outputs via the outlet, and in which any changes in lake mass were accounted

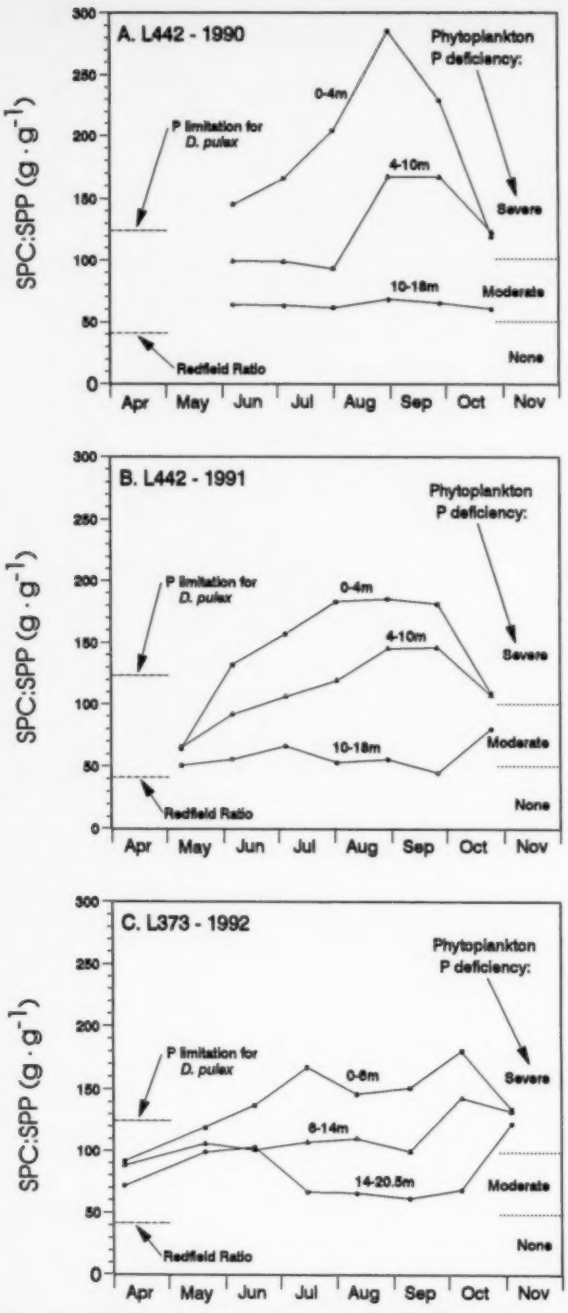


FIG. 5. Ratio of sestonic particulate carbon (SPC) to sestonic particulate phosphorus (SPP) for three depth zones approximating the midsummer epilimnion, the remainder of the photic zone (metalimnion), and the hypolimnion. (A)Lake 442, 1990 (0–4 m, 4–10 m, and 10–18 m). (B) Lake 442, 1991 (0–4 m, 4–10 m, and 10–18 m). (C) Lake 373, 1992 (0–6 m; 6–14 m, and 14–20.5 m). Phytoplankton P-deficiency limits are after Healey and Hendzel (1980); P limitation for *Daphnia pulex* is from Olsen et al. (1986).

for (e.g., Schindler et al. 1973, 1987). Over the long term, at increments of 1 yr, this may be a valid and useful approach. However, annual budgets may miss short-lived, but important, P-regeneration events such as are obviously occurring in Lakes 442 and 373. Closer inspection of results from some of the whole-lake eutrophication experiments may show the same phenomenon. For example, spikes in P standing stocks in Lake 227 can be greatly in excess of the amounts added artificially (Fig. 8). Short-term increases in the whole-lake mass of P in Lake 227 have been as high as 10 $kg \cdot wk^{-1}$, but the corresponding P-addition rate was only 1.1 $kg \cdot wk^{-1}$ (Cruikshank 1984).

Even when short-term analyses do show an exit of sestonic and/or dissolved P from the water column exceeding loss through the outlet, the conclusion that P is being removed to the sediments may still be inappropriate because shifts to other pools in the water column may also be important. Specifically, consumption of P by zooplankton or fish may be important at certain times (Scavia 1979; Taylor 1984; Sterner et al. 1992). Conversely, zooplankton or fish can also be important regenerators of P to the water column (Barlow and Bishop 1965; Peters 1975; Nakashima and Leggett 1980). The importance of nutrient cycling to or from larger organisms within the water column has largely been ignored at the ELA (except see Vanni and Findlay 1990), although its potential importance has been recognized (Levine and Schindler 1992). In this study, access to contemporaneous zooplankton data (Salki 1993; A. Salki, Department of Fisheries and Oceans, Winnipeg, MB, unpublished data), having good horizontal and vertical resolution, facilitated an initial assessment of the relative importance of zooplankton as a P source or sink.

Zooplankton

Phosphorus content of cladocerans and post-nauplial cyclopoids and calanoids was estimated from biomass data for Lake 442 (1990 and 1992), and Lake 373 (1992). Nauplii were excluded because they were probably also collected on the filters used for sestonic P determinations. Dry weight was computed as 7% of wet weight (A. Salki, personal communication), and P content was assumed to be 1% of dry weight. Phosphorus content of calanoids is generally reported to be lower than for cladocerans. The range reported is 0.41% P for *Eudiaptomus gracilis* to >1.5% P for some *Daphnia* species (Andersen and Hessen 1991; Sterner et al. 1992). Although P content differs among species, it has also been found that P content will remain relatively constant for a given species, regardless of changes in nutritional condition of its food organisms (Sterner et al. 1992). On average, cyclopoids, calanoids, and cladocerans composed 20, 55, and 25%, respectively, of the zooplankton biomass in Lakes 373 and 442.

The zooplankton phosphorus (ZP) pool was found to be small. On average, <5% of the water-column P was in zooplankton; 60% was accounted for by seston and 35% was in solution. The small fraction of P in the zooplankton pool is similar to values reported elsewhere (Prepas and Rigler 1982; Prepas and Vickery 1984; Elser and George 1993). Inclusion of the ZP pool in lakes 373 and 442 resulted in no change in temporal patterns in water-column P standing stocks (Fig. 9). The lack of evidence of any shifts of P from the seston or dissolved pool to zooplankton, or vice versa, is contrary to what might have been anticipated based on arguments

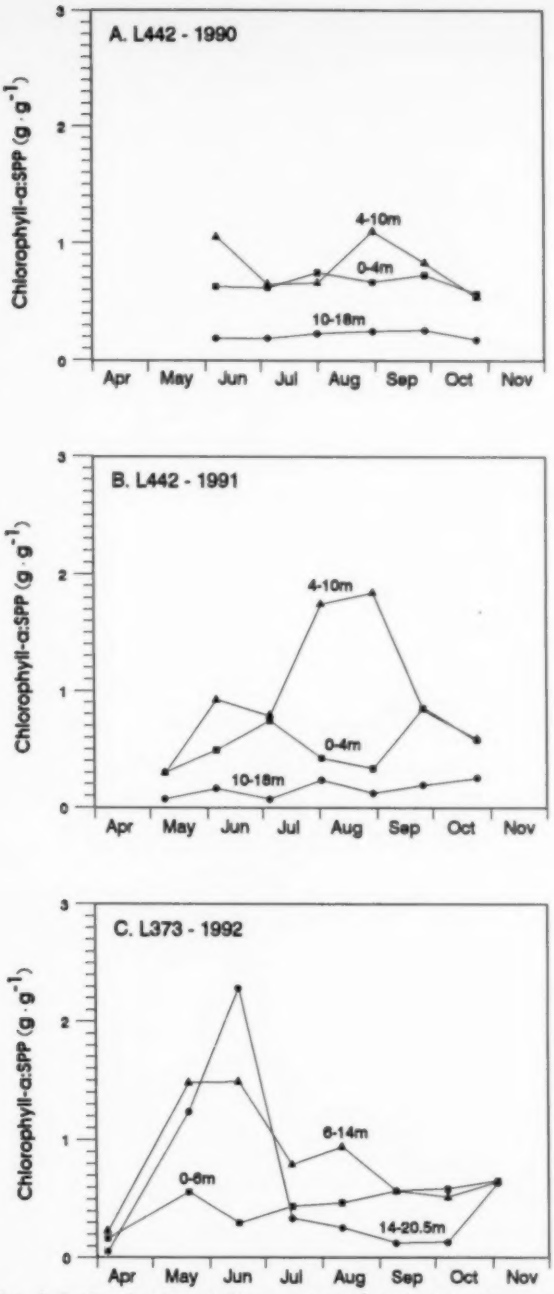


FIG. 6. Ratio of chlorophyll *a* to sestonic particulate phosphorus (SPP) for three depth zones approximating the midsummer epilimnion, the remainder of the photic zone (metalimnion), and the hypolimnion. (A) Lake 442, 1990 (0–4 m, 4–10 m, and 10–18 m). (B) Lake 442, 1991(0–4 m, 4–10 m, and 10–18 m). (C) Lake 373, 1992 (0–6 m, 6–14 m, and 14–20.5 m).

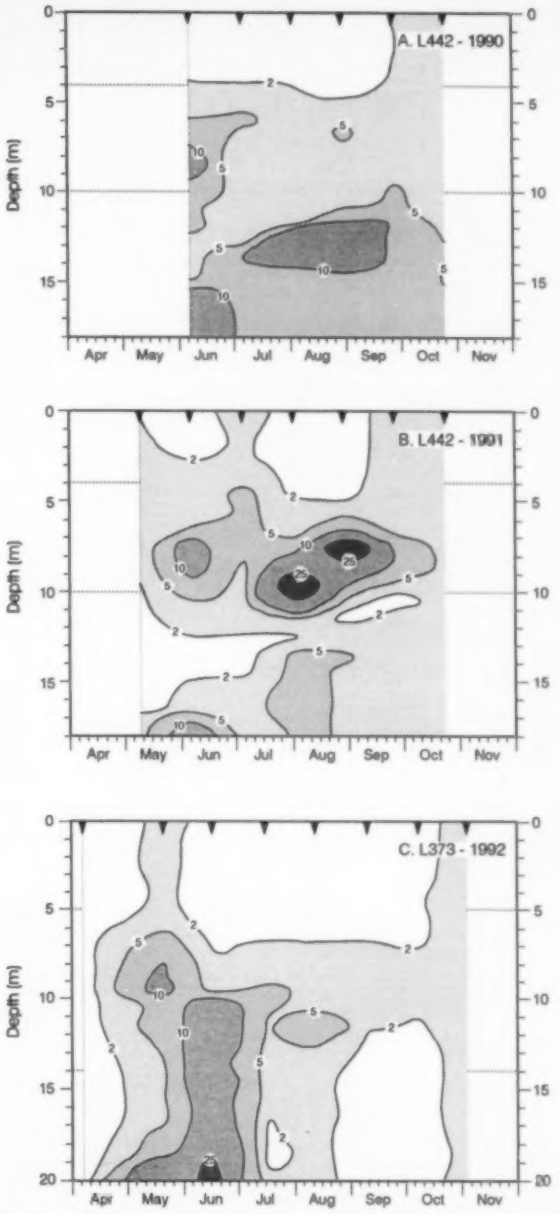


FIG. 7. Isopleth diagram of photosynthetic plankton biomass (chlorophyll *a*; $\mu g \cdot L^{-1}$) during the open-water season. (A) Lake 442, 1990. (B) Lake 442, 1991. (C) Lake 373, 1992. Lake 373 was ice-covered during the first sampling interval, April 5 – May 19.

by some authors (e.g., Sterner et al. 1992). In fact, zooplankton biomass in Lakes 442 and 373 appeared to remain relatively constant through most of the open-water season; moreover, storage in the zooplankton compartment was simply too small to provide an important source or sink of P to or from the seston and/or dissolved phase.

The soluble fraction of P that accumulated over the summer, particularly in the epilimnion and metalimnion (Fig. 1), was probably high molecular weight, refractory compounds (Lean 1973; Schindler et al. 1977; Elser and George 1993). Scavia (1979) suggested that these compounds were the end products of organic matter cycled several times through the food web. He, too, found that the largest accumulation in

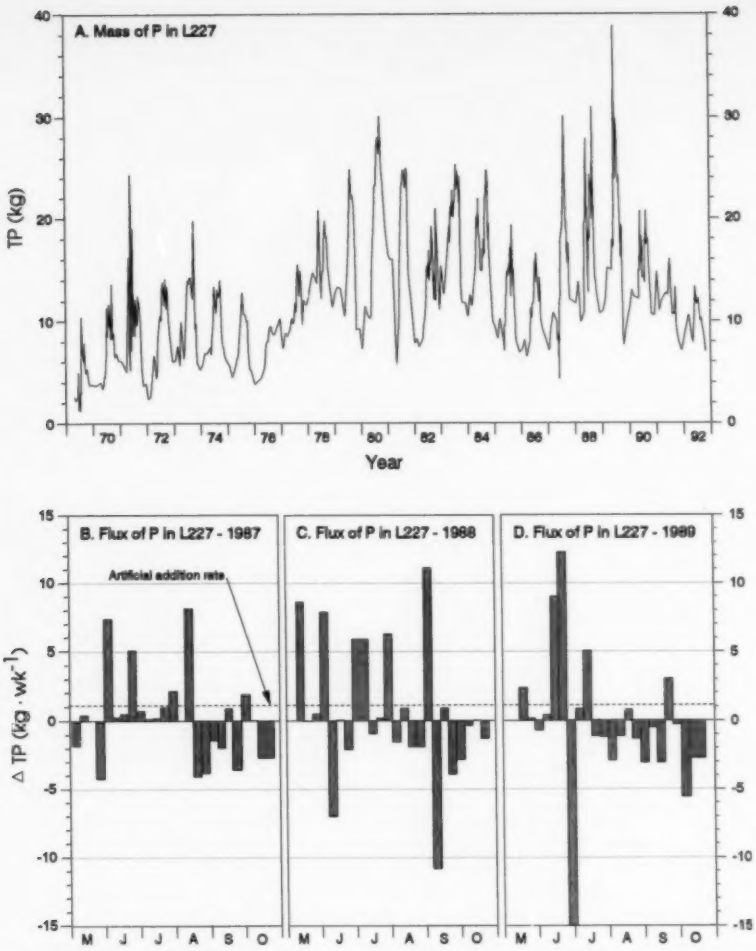

A. Mass of P in L227
TP (kg)
Year
B. Flux of P in L227 - 1987
C. Flux of P in L227 - 1988
D. Flux of P in L227 - 1989
Artificial addition rate
Δ TP (kg · wk⁻¹)
M J J A S O

FIG. 8. Mass of phosphorus (P) in Lake 227. (A) 1969–92. (B) Weekly changes in whole-lake total phosphorus (TP) content during three open-water seasons when P fluxes to the water column in excess of artificial addition rates were particularly large and frequent. These data are further to Schindler et al. (1987).

Lake Ontario was in late summer, and he believed that the P forms constituting this fraction were (as reported by Berman 1970) more resistant to enzymatic breakdown at certain times of the year, including August and September. Scavia (1979) concluded that a large fraction of soluble unreactive P (SUP) became available to the phytoplankton in spring and fall. This assessment cannot be made directly for Lakes 373 or 442 without soluble reactive P (SRP) data. However, Fig. 1A suggests, for the epilimnion and metalimnion, an inverse relationship between TDP and SPP; i.e., as what is assumed to be SUP accumulates, SPP decreases, and vice versa, although the relationship is not as obvious in Fig. 1B or 1C.

It has been repeatedly demonstrated that internal, fast-reaction, P cycling is essential for maintenance of water-column photosynthesis in ELA lakes (e.g., Table 8). The current comparative study, which emphasized P standing stocks, was not designed to provide any new information in that regard. However, some deductions can be made regarding the role played by zooplankton as a supplier of P to primary producers. Estimates of the proportion of photosynthetic requirements produced by zooplankton range from 12 (Nakashima and Leggett 1980) to 100% (Barlow and Bishop 1965). Peters (1975) calculated a zooplankton excretion rate of 2.8 mg $P \cdot m^{-2} \cdot d^{-1}$ in ELA Lake 302. This excretion rate, applied to Lake 373 or Lake 442, would be 2–4 times that required for photosynthesis and 15–60 times the net external supply rate of P to these lakes. Zooplankton excretion cannot be placed in exact perspective relative to other fast-reaction, P-recycling routes, but potential exists for zooplankton to function as major suppliers of P to photosynthesizers in Lakes 373 and 442, despite the relatively small proportion of the water-column TP pool constituted by ZP.

Phytoplankton in Lakes 373 and 442 were severely P deficient (Healey and Hendzel 1980; Fig. 5), particularly in the upper reaches of the photic zone; P deficiency worsened as the summer progressed. In early spring and late fall, P deficiency was minimal. Water-column P attained a maximum in spring; however, P content of the water column in late fall

TABLE 8. Photosynthetic uptake rates ($\mu g \cdot d^{-1} \cdot m^{-2}$) of carbon (C) and phosphorus (P) in Lakes 442 and 373 during the open-water season. Gross and net external supply rates of P (from Table 5) are included for comparison. Phosphorus fixed by photosynthesis was obtained by applying the P/C ratio of epilimnetic seston (calculated at 4-wk intervals) to daily estimates of photosynthetic C uptake rates.

	Photosynthetic uptake		External P supply	
	C	P	Gross	Net
Lake 442				
1990 (June 6 – Oct. 23)	115 000	540	70	45
1991 (May 8 – Oct. 22)	114 000	790	128	55
1992 (May 13 – Nov. 2)	128 000	1010	314	188
Lake 373				
1991 (May 22 – Oct. 8)	98 500	630	61	49
1992 (May 20 – Nov. 2)	153 000	1030	142	116

was usually at a minimum. This pattern suggests that some factor(s) other than gross supply of P are important determinants of seasonal differences in algal nutrient status. These may include: (1) seasonal differences in hydrolyzability of P compounds (see above); or, (2) low availability of light in late fall (Shearer et al. 1985). Although phytoplankton cells in the surface waters were clearly severely P limited during most of the growing season, seston became less and less P deficient with depth. In fact, particles of seston in the hypolimnion were rarely severely P deficient (Fig. 5).

The data reported here provide evidence of strong bottom-up control of the zooplankton dynamics in Lakes 373 and 442. Zooplankton were most concentrated in the metalimnion, followed by the hypolimnion (Table 9). This was not likely a function of negative phototoaxis; there was little diurnal vertical migration in these lakes (A. Salki, unpublished data). Attraction of zooplankton to the deeper regions of Lakes 442 and 373 was probably a result of higher concentrations of food particles there (Fig. 7), and because these particles were more nutritious than those in the epilimnion (Fig. 3 and 5). Live phytoplankton residing in the mid-depths of Lakes 442 and 373 are predominantly edible chrysophytes (Hendzel et al. 1994), and the P content of these potential food particles is frequently three to four times higher in the bottom waters than in the epilimnion (Fig. 5).

A predominance of nutritionally deficient algae, such as is characteristic of Lakes 373 and 442, should give advantage to the zooplankton species that can produce the largest amount of biomass per unit P available (Sterner et al. 1992). As noted above, P requirements of copepods are, on average, only half that of cladocerans, and calanoids and cyclopoids did, in fact, dominate Lakes 373 and 442 (Table 9). It could also follow that the relative vertical distribution of zooplankters should reflect differences in ability of species to adapt to nutrient-poor conditions; specifically, copepods, which require less P, should be better able than cladocerans to adapt to the nutrient-poor conditions of the epilimnion. Further, from a temporal perspective, the relative abundance

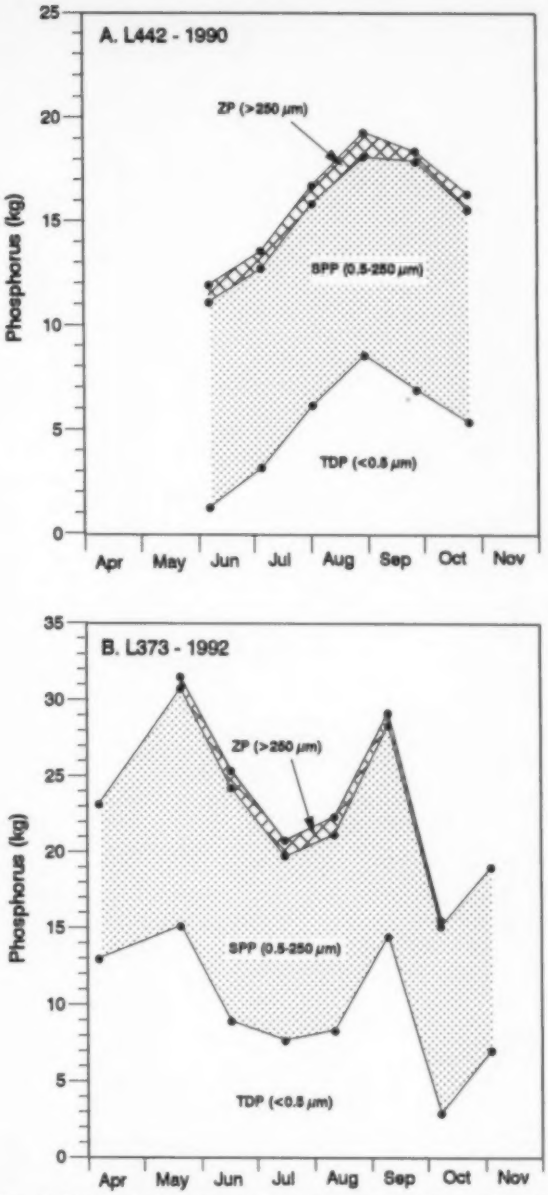


FIG. 9. Mass of phosphorus (P) in the water column, showing the relative contributions of total dissolved phosphorus (TDP), sestonic particulate phosphorus (SPP), and P in crustacean zooplankton (ZP). (A) Lake 442, 1990. (B) Lake 373, 1992.

of cladocerans should decrease at times of maximum deterioration in algal nutrient status. Olsen et al. (1986) concluded that *Daphnia pulex* could become P limited if its main diet contained <6-8 μg P·mg^{-1} C. Based on this criterion, cladocerans would avoid the epilimnia of Lakes 373 and 442 in favor of the more nutrient-rich metalimnion or hypolimnion (Fig. 5). In fact, there are fewer cladocerans in the surface waters compared with the mid-depths; however, note that the lowest densities of cladocerans occurred in the bottom waters (Table 9).

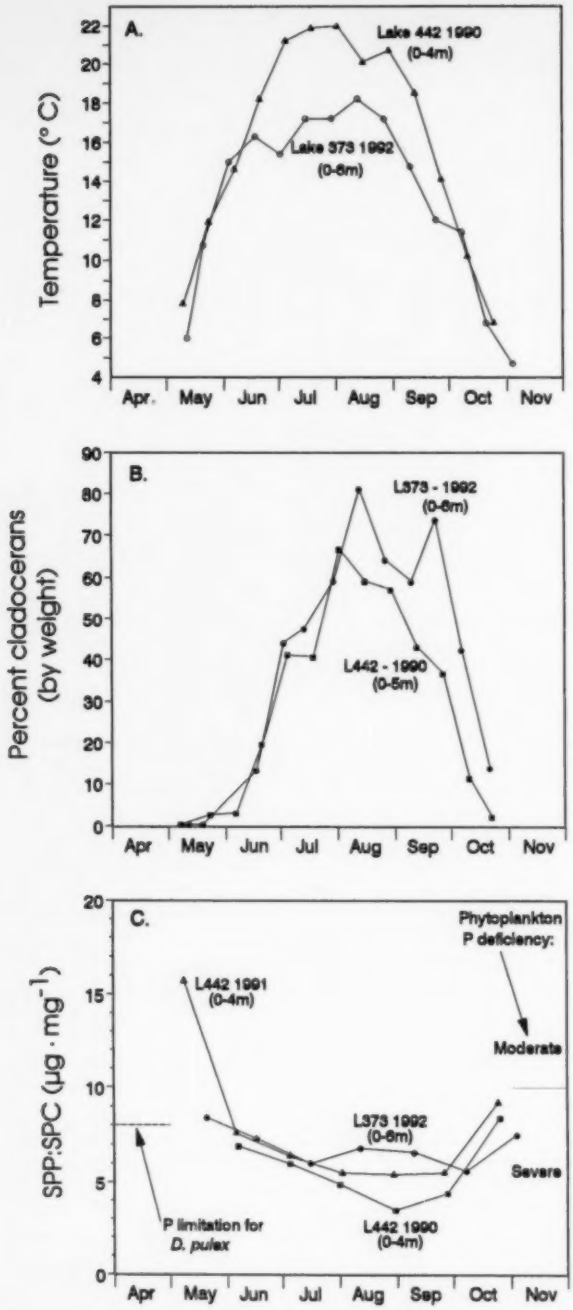


FIG. 10. Epilimnetic temperature, zooplankton composition, and phytoplankton nutrient status for Lakes 373 and 442. (A) Temperature. (B) Percent cladocerans, excluding nauplii. (C) Phytoplankton nutrient status (sestonic particulate phosphorus (SPP) / sestonic particulate carbon (SPC)).

Although cladocerans preferred mid-depths, they were apparently better able to cope with severe epilimnetic P deficiency than the calanoids and especially the cyclopoids, which are mostly carnivores (Table 10). The relative abundance

TABLE 9. Average biomass (wet weight) of post-nauplial cyclopoids, post-nauplial calanoids, and cladocerans in selected depth zones during the open-water season for Lake 442 in 1990 and 1992 and Lake 373 in 1992.

	Biomass ($mg \cdot m^{-3}$)			
Depth (m)	Cyclopoids	Calanoids	Cladocerans	All
		Lake 442, 1990		
0–5	68.8	289	152	510
5–18	214	454	221	889
Whole lake	144	375	188	707
		Lake 442, 1992		
0–5	71.5	285	146	503
5–9	183	620	204	1007
9–18	116	240	52.5	409
Whole lake	115	375	143	633
		Lake 373, 1992		
0–6	16.1	164	91.7	272
6–12	112	267	120	499
12–20.5	146	256	60.4	462
Whole lake	77.2	219	93.7	390

TABLE 10. Average ratios of zooplankton biomass concentrations in the epilimnion, metalimnion, and hypolimnion relative to the metalimnion during the open-water season of 1992.

Depth (m)	Cyclopoids	Calanoids	Cladocerans	All
		Lake 442		
0–5	0.39	0.46	0.72	0.50
5–9	1.00	1.00	1.00	1.00
9–18	0.63	0.39	0.26	0.41
		Lake 373		
0–6	0.14	0.61	0.76	0.55
6–12	1.00	1.00	1.00	1.00
12–20.5	1.30	0.96	0.50	0.93

of cladocerans appeared to be negatively correlated with the degree of algal P deficiency (Fig. 10B and 10C). Large grazers having high requirements for P probably drove the epilimnetic seston into a state of extreme P deficiency (Sterner et al. 1992).

Zooplankters that contain less P may not be more efficient in P deficient environments. Cladocerans that require more P probably have evolved more efficient or selective P assimilation and/or retention mechanisms. For example, Olsen et al. (1986) concluded that *Daphnia* was able to retain all ingested P when C/P ratios of its food were too high. Cladocerans also may be subject to another requirement that takes precedence over nutritional conditions, forcing them to reside in shallow waters. For example, temperature conditions may be an important determinant of cladoceran population dynamics in Lakes 442 and 373 (Fig. 10A cf. 10B; see also Patalas and Salki 1984; Lehman and Caceres 1993).

Fish

No fish data were available for Lake 373 or Lake 442 from which seasonal P budgets could be derived. However, certain assumptions were made to estimate their probable importance (Mills and Chalanchuk 1987 for Lake 226SW; K. Mills and D. Bodaly, Department of Fisheries and Oceans, Winnipeg, MB, personal communication). Total fish biomass (including minnows) in Lakes 373 and 442 was taken to average 60 $kg \cdot ha^{-1}$ (cf. Fraser 1981: 35.2–50.8 $kg \cdot ha^{-1}$). Fish phosphorus (FP) in Lakes 442 and 373 was estimated to be 7680 and 13 100 g, respectively, using a wet weight to dry weight conversion factor of 0.2 and P content of 4% of dry weight (Kitchell et al. 1975).

Average whole-lake partitioning of P among the four water-column compartments considered here is summarized in Table 11. Seston was the largest fraction (≈40%), followed by fish (30–35%), the dissolved phase (≈25%), and zooplankton (2–4%); no single fraction predominated. The relative contributions would probably differ considerably if the epilimnion, metalimnion, and hypolimnion were considered separately. For example, the bulk of cyprinid FP is probably in the surface waters, whereas sestonic P would be a higher proportion of the total in both the hypolimnion and metalimnion. The ZP fraction would probably be higher in the metalimnion and hypolimnion than in the epilimnion, although it still is only a minor contribution to the total. The fraction of total water-column P estimated to be FP was considerably less than in eutrophic Lake Wingra, Wisconsin (74%: Kitchell et al. 1975).

The fish compartment in either Lake 442 or Lake 373 was large enough to store or supply the P shifting from or to the seston or dissolved phases that was unaccounted for by external inputs or outputs (Table 6; Fig. 4). However, shifts of P to and from the seston and dissolved phase did not correspond in a logical way with probable patterns of P accumulation and release from the fish pool. For example, during June, July, and August there should be net fish growth (K. Mills, personal communication) and net accumulation of FP at the same time as P is increasing in solution and the seston (Fig. 1). More importantly, shifts to and from the FP compartment large enough to account for changes in seston and dissolved P of the magnitudes illustrated in Figs. 1 and 4 would imply almost total mortality of the fish population during the open-water season. Hence, such a scenario is impossible.

Conclusion

A high degree of uncertainty is associated with the FP estimates that were used here, but the error in the estimates probably does not exceed 100%. Certainly, FP is not in error by an order of magnitude, which was approximately the upwards adjustment in biomass that would be required in order to accommodate the P shifts into the smaller size fractions without involving unreasonably high fish mortality rates. Therefore, the large short-term changes in water-column P standing stocks unaccounted for by net external inputs were probably the result of P regeneration from, and P deposition to, the sediments.

The following open-water scenario is possible. Less than half of the P added to the water column in early spring is attributable to external inputs. The P gain by the water column at ice-out (Fig. 1C) is mostly sestonic and tends to accumulate in the metalimnion. At this time, algal cells in the metalimnion and hypolimnion apparently manufacture chlorophyll at a high rate relative to those in the epilimnion or relative to other times of the year (Fig. 6C). In the deeper waters, algae are charged with nutrients and respond quickly to maximum light and warmer temperatures after the ice thaws. Resuspension of algal cells from deep zones may not necessarily be physical, i.e., a function of spring circulation. Mobile algal cells on the bottom may extract P from nutrient-rich interstitial water prior to rising into the water column where they seek out optimal light and temperature conditions. The spring turnover period is brief and, in the case of Lake 442, even incomplete. During the more vigorous, protracted turnover in fall, no addition of P to the water column occurs. In fact, large quantities of P, particularly hypolimnetic SPP, disappear from the water column at this time.

Having concluded above that residual P did not originate from P shifts to or from zooplankton or fish, it is probable that the late spring/early summer clearwater phase, when SPP and TDP are at minimum (Fig. 1), is primarily a function of sedimentation. Large quantities of detrital seston are visible in the hypolimnion during late summer (Fig. 1), but such accumulations are not evident during the clear-water phase. These observations may reflect a two-step process whereby water-column P removed in June–July is first deposited in shallow sediments, mainly as fish fecal pellets. High densities of small fecal pellets, presumably from minnows, have been observed in the shallows of Lakes 442 and 373 in early summer (M. Turner, Department of Fisheries and Oceans, Winnipeg, MB, unpublished data). Microbial degradation of these fecal pellets could provide an important source of P for fuelling epilimnetic seston production during the summer and may partially compensate for the summertime accumulation of refractory SUP. Alternatively, significant amounts of biologically available P could be resupplied to the epilimnion during summer stratification simply by resuspension of shallow surficial sediments (Dillon et al. 1990). As mentioned above, seston produced during the summer does ultimately accumulate as detritus in the hypolimnion and on the bottom.

By fall overturn, temperature and light conditions have degraded sufficiently that only minimal response occurs to autumnal circulation as reflected in the surface seston.

TABLE 11. Average partitioning (%) of phosphorus (P) among the four major compartments in the water columns of Lakes 442 and 373 during the open-water season. TDP = total dissolved phosphorus, <0.5 μm; SPP = suspended particulate (sestonic) phosphorus, 0.5–250 μmm; ZP = zooplankton (cladoceran + copepod, excluding nauplii) P; FP = total fish P.

	Lake 442		Lake 373
	1990	1992	1992
TDP	22.2	23.8	26.0
SPP	42.0	43.6	36.5
ZP	3.5	2.6	2.4
FP	32.3	30.0	35.1

Apparently, fall overturn neither increases availability of P nor resuspends nutritionally favored resting cells from the bottom waters. In fact, the rapid reduction in hypolimnetic seston during late fall suggests an active retreat of resting cells to the bottom sediments.

Acknowledgments

I am indebted to the ELA research team for intellectual and physical support. I thank the following individuals for their help: D. Cruikshank, G. McCullough, K. Beaty, M. Lyng, M. Stainton, R. Schade, J. Boughen, G. Regehr, B. Hauser, T. Lyng, A. McHutchon, E. DeBruyn, E. Schindler, L. Hendzel, D. Findlay, A. Salki, K. Mills, and S. Kasian. D. Laroque typed the manuscript. N. Strange did the graphics. M. Turner, R. Hecky, K. Patalas, D. Rosenberg, A. Salki, R. Sterner, and an anonymous reviewer provided valuable comments on the manuscript.

References

ANDERSEN, T., AND D.O. HESSEN. 1991. Carbon, nitrogen, and phosphorous content of freshwater zooplankton. Limnol. Oceanogr. 36: 807–814.

BARLOW, J.P., AND J.W. BISHOP. 1965. Phosphate regeneration by zooplankton in Cayuga Lake. Limnol. Oceanogr. 10: R15–R24.

BEATY, K.G., AND M.E. LYNG. 1989. Hydrometeorological data for the Experimental Lakes Area, northwestern Ontario, 1982 to 1987. Can. Data Rep. Fish. Aquat. Sci. 759: 280 p.

BERMAN, T. 1970. Alkaline phosphatases and phosphorus availability in Lake Kinneret. Limnol. Oceanogr. 15: 663–674.

CAMPBELL, P. 1993a. Comparison of two methods commonly used at the Experimental Lakes Area for collecting chemistry samples from vertically stratified lakes. Can. Tech. Rep. Fish. Aquat. Sci. 1881: 20 p.

CAMPBELL, P. 1993b. Lake variation and climate change study: ELA lakes, 1986–1990. I. Study rationale and lake selection criteria. Can. Tech. Rep. Fish. Aquat. Sci. 1897: 5 p.

CARACO, N.F., J.J. COLE, AND G.E. LIKENS. 1991. A cross-system study of phosphorus release from lake sediments, p. 241–258. *In* J. Cole, G. Lovett, and S. Findlay [ed.] Comparative analyses of ecosystem patterns, mechanisms, and theories. Springer-Verlag, New York.

CARPENTER, S.R., K.L. COTTINGHAM, AND D.E. SCHINDLER. 1992. Biotic feedbacks in lake phosphorus cycles. Trends Ecol. Evol. 7(10): 332–336.

CRUIKSHANK, D.R. 1984. Whole lake chemical additions in the Experimental Lakes Area, 1969–1983. Can. Data Rep. Fish. Aquat. Sci. 449: 23 p.

CRUIKSHANK, D.R., P. CAMPBELL, S.E.M. KASIAN, E.U. SCHINDLER, AND G.K. MCCULLOUGH. 1993. Lake variation and climate change study: ELA lakes, 1986–1990. III. Field observations, hydrological, light, and temperature measurements. Can. Data Rep. Fish. Aquat. Sci. 908: 94 p.

DILLON, P.J., R.D. EVANS, AND L.A. MOLOT. 1990. Retention and resuspension of phosphorus, nitrogen, and iron in a central Ontario lake. Can. J. Fish. Aquat. Sci. 47: 1269–1274.

ELSER, J.J., AND N.B. GEORGE. 1993. The stoichiometry of N and P in the pelagic zone of Castle Lake, California. J. Plankton Res. 15: 977–992.

EMERSON, S., AND R. HESSLEIN. 1973. The distribution and uptake of artificially introduced radium-226 in a small lake. J. Fish. Res. Board Can. 30: 1485–1490.

FEE, E.J. 1978. Studies of hypolimnion chlorophyll peaks in the Experimental Lakes Area, northwestern Ontario. Can. Fish. Mar. Serv. Tech. Rep. 754: 21 p.

FEE, E.J., J.A. SHEARER, AND D.R. DECLERCQ. 1977. *In vivo* chlorophyll profiles from the Experimental Lakes Area, northwestern Ontario. Can. Fish. Mar. Serv. Tech. Rep. 703: 136 p.

FRASER, J.M. 1981. Estimates of the standing stocks of fishes in four small Precambrian Shield lakes. Can. Field-Nat. 95: 137–143.

HEALEY, F.P., AND L.L. HENDZEL. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Can. J. Fish. Aquat. Sci. 37: 442–453.

HECKY, R.E., P. CAMPBELL, AND L.L. HENDZEL. 1993. The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. Limnol. Oceanogr. 38: 709–724.

HENDZEL, L.L., D.L. FINDLAY, E.U. SCHINDLER, AND P. CAMPBELL. 1995. Lake variation and climate change study: ELA lakes, 1986–1990. IV. Phytoplankton photosynthesis, nutrient status, and species composition and enumeration data. Can. Data Rep. Fish. Aquat. Sci. (In press)

HUTCHINSON, G.E. 1957. A treatise on limnology. Vol. 1. Geography, physics and chemistry. John Wiley & Sons, New York. 1015 p.

KITCHELL, J.F., J.F. KOONCE, AND P.S. TENNIS. 1975. Phosphorus flux through fishes. Int. Ver. Theor. Angew. Limnol. Verh. 19: 2478–2484.

LEAN, D.R.S. 1973. Movements of phosphorus between its biologically important forms in lake water. J. Fish. Res. Board Can. 30: 1525–1536.

LEHMAN, J.T., AND C.E. CACERES. 1993. Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. Limnol. Oceanogr. 37: 879–891.

LEVINE, S.N., AND D.W. SCHINDLER. 1980. Radiochemical analysis of orthophosphate concentrations and seasonal changes in the flux of orthophosphate to seston in two Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 37: 479–487.

LEVINE, S.N., AND D.W. SCHINDLER. 1989. Phosphorus, nitrogen, and carbon dynamics of Experimental Lake 303 during recovery from eutrophication. Can. J. Fish. Aquat. Sci. 46: 2–10.

LEVINE, S.N., AND D.W. SCHINDLER. 1992. Modification of the N:P ratio in lakes by *in situ* processes. Limnol. Oceanogr. 37: 917–935.

LINSEY, G.A., D.W. SCHINDLER, AND M.P. STAINTON. 1987. Atmospheric deposition of nutrients and major ions at the Experimental Lakes Area in northwestern Ontario, 1970 to 1982. Can. J. Fish. Aquat. Sci. 44(Suppl. 1): 206–214.

MCCULLOUGH, G.K., AND P. CAMPBELL. 1993. Lake variation and climate change study: ELA lakes, 1986–1990. II. Watershed geography and lake morphology. Can. Tech. Rep. Fish. Aquat. Sci. 1898: 29 p.

MILLS, K.H., AND S.M. CHALANCHUK. 1987. Population dynamics of lake whitefish (*Coregonus clupeaformis*) during and after fertilization of Lake 226, the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. 44(Suppl. 1): 55–63.

NAKASHIMA, B.S., AND W.C. LEGGETT. 1980. The role of fishes in the regulation of phosphorus availability in lakes. Can. J. Fish. Aquat. Sci. 37: 1540–1549.

NEWBURY, R.W., AND K.G. BEATY. 1980. Water renewal efficiency of watershed lake combinations in the ELA region of the Precambrian Shield. Can. J. Fish. Aquat. Sci. 37: 335–341.

OLSEN, Y., A. JENSEN, H. REINERTSEN, K.Y. BORSHEIM, M. HELDAL, AND A. LANGELAND. 1986. Dependence of the rate of release of phosphorus by zooplankton on the P/C ratio in the food supply, as calculated by a recycling model. Limnol. Oceanogr. 31: 34–44.

PATALAS, K., AND A. SALKI. 1984. Effects of impoundment and diversion on the crustacean plankton of Southern Indian Lake. Can. J. Fish. Aquat. Sci. 41: 613–637.

PETERS, R.H. 1975. Phosphorus regeneration by natural populations of limnetic zooplankton. Int. Ver. Theor. Angew. Limnol. Verh. 19: 273–279.

PREPAS, E.E., AND F.H. RIGLER. 1982. Improvements in quantifying the phosphorus concentration in lake water. Can. J. Fish. Aquat. Sci. 39: 822–829.

PREPAS, E.E., AND J. VICKERY. 1984. Contribution of particulate phosphorus (>250 μm) to the total phosphorus pool in lake water. Can. J. Fish. Aquat. Sci. 41: 351–363.

SALKI, A.G. 1992. Lake variation and climate change study: crustacean plankton of a lake size series in the Red Lake District, northwest Ontario, 1987–1989 and Lake Nipigon, 1989. Can. Data Rep. Fish. Aquat. Sci. 862: 30 p.

SALKI, A.G. 1993. Lake variation and climate change study: VII. Crustacean plankton of a lake flushing rate series in the Experimental Lakes Area, northwestern Ontario, 1987–1990. Can. Data Rep. Fish. Aquat. Sci. 880: 74 p.

SCAVIA, D. 1979. Examination of phosphorus cycling and control of phytoplankton dynamics in Lake Ontario with an ecological model. J. Fish. Res. Board Can. 36: 1336–1346.

SCHINDLER, D.W. 1975. Whole-lake eutrophication experiments with phosphorus, nitrogen, and carbon. Int. Ver. Theor. Angew. Limnol. Verh. 19: 3221–3231.

SCHINDLER, D.W., AND E.J. FEE. 1974. Experimental Lakes Area: whole-lake experiments in eutrophication. J. Fish. Res. Board Can. 31: 937–953.

SCHINDLER, D.W., R. HESSLEIN, AND G. KIPPHUT. 1977. Interactions between sediments and overlying waters in an experimentally eutrophied Precambrian Shield lake, p. 235–243. *In* H.L. Golterman [ed.] Interactions between sediments and freshwater: Proceedings of an International Symposium, September 1976, Amsterdam. Dr. W. Junk Publishers, The Hague and Pudoc, Wageningen.

SCHINDLER, D.W., R.H. HESSLEIN, AND M.A. TURNER. 1987. Exchange of nutrients between sediments and water after 15 years of experimental eutrophication. Can. J. Fish. Aquat. Sci. 44(Suppl. 1): 26–33.

SCHINDLER, D.W., H. KLING, R.V. SCHMIDT, J. PROKOPOWICH, V.E. FROST,

R.A. Reid, and M. Capel. 1973. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

Schindler, D.W., D.R.S. Lean, and E.J. Fee. 1975. Nutrient cycling in freshwater ecosystems, p. 96–106. *In* D.E. Reichle, J.F. Franklin, and D.W. Goodall [ed.] Productivity of World Ecosystems; Proceedings of a Symposium, Aug. 31 – Sept. 1, 1972, Seattle, WA. National Academy of Sciences, Washington, DC.

Schindler, D.W., R.W. Newbury, K.G. Beaty, and P. Campbell. 1976. Natural water and chemical budgets for a small Precambrian lake basin in central Canada. J. Fish. Res. Board Can. 33: 2526–2543.

Shearer, J.A. 1978. Two devices for obtaining water samples integrated over depth. Can. Fish. Mar. Serv. Tech. Rep. 772: 9 p.

Shearer, J.A., E.R. DeBruyn, D.R. DeClercq, D.W. Schindler, and E.J. Fee. 1985. Manual of phytoplankton primary production methodology. Can. Tech. Rep. Fish. Aquat. Sci. 1341: 58 p.

Stainton, M.P., M.J. Capel, and F.A.J. Armstrong. 1977. The chemical analysis of fresh water. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25: 180 p.

Sterner, R.W., J.J. Elser, and D.O. Hessen. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. Biogeochemistry 17: 49–67.

Taylor, W.D. 1984. Phosphorus flux through epilimnetic zooplankton from Lake Ontario: relationship with body size and significance to phytoplankton. Can. J. Fish. Aquat. Sci. 41: 1702–1712.

Vanni, M.J., and D.L. Findlay. 1990. Trophic cascades and phytoplankton community structure. Ecology 71: 921–937.

Effects of Lake Size on Nutrient Availability in the Mixed Layer during Summer Stratification[1]

E.J. Fee, R.E. Hecky, G.W. Regehr, L.L. Hendzel, and P. Wilkinson

Department of Fisheries and Oceans, Central and Arctic Region, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Fee, E.J., R.E. Hecky, G.W. Regehr, L.L. Hendzel, and P. Wilkinson. 1994. Effects of lake size on nutrient availability in the mixed layer during summer stratification. Can. J. Fish. Aquat. Sci. 51: 2756–2768.

Fluxes to the summer mixed layer of N, Si, and P were estimated in a size series of northwestern Ontario Canadian Shield lakes. Increasing turbulence caused upward fluxes through the thermocline to increase with lake size for nutrients that increased in concentration below the thermocline (soluble reactive Si, total inorganic N, and NO_3^-; but not total N or any form of P). Precipitation and terrestrial runoff were equally important sources of N and P in all but very small lakes (<100 ha), where precipitation supplied much more than runoff. Runoff was the only important source of Si, except in very large lakes (> 100 000 ha) where mixing through the thermocline was important. N_2-fixation was unimportant except in intermediate-sized lakes (700–2000 ha). Si fluxes nearly equaled phytoplankton requirements, but N and P were below requirements, and recycling within the mixed layer must be the most important source of these nutrients. N and P deficits increased progressively with lake size, implying that the efficiency of nutrient recycling increased with lake size; mixed layers in large lakes are more turbulent and thicker than in small lakes and these processes increase the probability of nutrient regeneration within the mixed layer.

Les flux de N, de Si et de P vers la couche de mélange estivale ont été estimés dans des lacs de différentes tailles du Bouclier canadien dans le nord-ouest de l'Ontario. Une turbulence accrue donne lieu à une augmentation proportionnelle à la taille des lacs des flux ascendants dans la thermocline dans le cas des éléments nutritifs dont la concentration augmente sous la thermocline (Si réactif soluble, N inorganique total, et NO_3^-); mais non le N total et aucune forme de P). Les précipitations et le ruissellement de surface étaient des sources de N et de P d'égale importance dans tous les lacs, sauf dans les très petits (<100 ha), où la contribution des précipitations étaient beaucoup plus importante à cet égard. Le ruissellement était la seule source importante de Si, sauf sans les très grands lacs (> 100 000 ha), où le mélange dans la thermocline apportait une contribution importante. La fixation du N_2 n'était pas importante sauf dans les lacs de taille intermédiaire (700–2 000 ha). Les flux de Si satisfaisaient presque les besoins du phytoplancton alors que ceux de N et de P étaient insuffisants, le recyclage dans la couche de mélange assurant probablement le principal apport de ces deux derniers éléments. Les carences en N et en P allaient en s'accroissant avec la taille des lacs, ce qui implique que la contribution du recyclage des éléments nutritifs s'accroît avec la taille des lacs; en effet, les couches de mélanges des grands lacs sont plus turbulentes et plus épaisses que celles des petits lacs, ce qui accroît les possibilités de régénération des éléments nutritifs dans la couche de mélange.

Received September 21, 1993
Accepted July 12, 1994
(J12098)

Reçu le 21 septembre 1993
Accepté le 12 juillet 1994

When Johnson and Vallentyne (1971) introduced the Experimental Lakes Area (ELA) program in the scientific literature, they clearly recognized that extrapolation of results obtained from the observation and manipulation of very small lakes to larger, more economically important ones was a fundamental assumption of ELA's design. They presented several examples of how a lake's size might affect critical limnological processes and stated that these "... must be taken into account in any extrapolation." Yet for nearly two decades, ELA results have been extrapolated to larger lakes without any explicit consideration of such effects. The Northwest Ontario Lake Size Series (NOLSS) program (Fee and Hecky 1992) was designed to remedy this deficiency; specifically, the purpose of NOLSS is to investigate physical gradients associated with lake size and to determine their biological significance.

In an initial NOLSS publication, Fee et al. (1992) reported that annual rates of phytoplankton photosynthesis (PP) per unit of lake surface area (i.e., areal PP) increased progressively with lake size simply because larger lakes were ice free for longer periods and had thicker mixed layers than small lakes. In contrast, these authors showed that annual rates of PP per unit volume of the mixed layer (volumetric PP) varied with lake size in a bell-shaped pattern, i.e., rates in the smallest and largest lakes (29 ha ELA Lake 373 and 8×10^6 ha Lake Superior, respectively) were low and similar, whereas midsized lakes had rates nearly an order of magnitude greater. Fee et al. (1992) hypothesized that this pattern resulted from systematic changes of turbulence and water temperature with increasing lake size. According to this hypothesis, the increasing intensity of turbulence with

[1]This is one in a series of papers describing work of the Freshwater Institute Science Laboratory on a lake-size series in Northwest Ontario. It is also a contribution to the series honoring the 25th anniversary of the Experimental Lakes Area.

lake size (Ward 1977; Quay et al. 1980) stimulates volumetric PP by increasing nutrient availability in the mixed layer, but decreasing water temperature with increasing lake size (Fee and Hecky 1992) simultaneously depresses it; the opposite effects of these two gradients on PP results in optimum conditions for PP in midsized lakes. This paper investigates one of the basic assumptions of this hypothesis: viz., that the increasing intensity of turbulence with lake size stimulates PP by making nutrients more available within the mixed layer.

It is well documented that algal growth and biomass in Canadian Shield lakes is limited by nutrients; more specifically, PP is primarily phosphorus (P) limited (Schindler 1977; Fee 1979; Hecky and Kilham 1987; Hecky et al. 1993; and especially S. Guildford and L. Hendzel, Department of Fisheries and Oceans, Winnipeg, MB, unpublished data for the NOLSS lakes).Theoretically, turbulence should be positively and causally related to nutrient availability in the mixed layer because: (1) more turbulent mixed layers retain particles longer, and thus recycle nutrients more effectively and (2) turbulence is the physical process responsible for the upward transport of nutrients through the summer thermocline. The second mechanism is more conditional than the first, however, because the turbulent (mixing) flux through the thermocline is not solely a function of the intensity of turbulence. That is, the flux of a substance S through a plane at depth z is

$$(1)\quad \text{Flux} = K_z \frac{dS}{dz}$$

where K_z is the coefficient of vertical eddy diffusion (i.e., turbulence). Hence, turbulence can result in a net upward flux to the mixed layer only if the concentration of S increases with depth in the region of the thermocline.

In this paper, we examine all major nutrient fluxes to the summer mixed layer in a size series of hydrologically and morphometrically similar lakes, during the period 1986–1991. Our purpose is to compare the magnitude of the only flux that depends explicitly on lake size, the turbulence-mediated upward flux through the summer thermocline, with fluxes that are independent of lake size: precipitation, terrestrial runoff, and N_2-fixation. We then assess the ecological importance of these fluxes by comparing them with the nutrient requirements of algae residing in the mixed layer.

Study Sites

Table 1 summarizes morphometric features of the study lakes and defines morphometric symbols used throughout the text. All the lakes are located on the Canadian Shield in northwestern Ontario, have water renewal times >5 yr, and are deep enough to fully stratify during the summer. Except for Lakes Nipigon and Superior, whose basins are sparsely populated, there are no permanent residents in the drainage basins of the lakes. More detailed descriptions are given by Fee and Hecky (1992) and Fee et al. (1992).

Methods

Unless otherwise stated, field and laboratory methods follow Fee et al. (1989) and Stainton et al. (1977). Temperature–depth stratification was measured with an electronic temperature logger (R. Brancker Research Ltd., Ottawa, ON;

TABLE 1. Summary of morphometric features of the study lakes. Depth profiles of chemical concentrations were not measured in the lakes marked with an asterisk. A_0, lake surface area (net water area, not including the area of islands); A_d, area of the terrestrial drainage basin (not including the lake area), τ_w, nominal water renewal time, calculated from lake volume, total watershed area, and maps of mean annual runoff; z_m, maximum depth; $\bar{z}$, mean depth.

	A_0 (ha)	A_d (ha)	τ_w (yr)	z_m (m)	$\bar{z}$ (m)
ELA					
Lake 373	29	54	13.5	21	10.3
NOLSS					
Green	89	234	8.6	19	7.7
Orange*	167	1 100	7.8	29	14.4
Linge	706	2 980	6.7	23	8.4
Musclow	2 220	32 850	5.0	46	19.2
Sydney	5 750	46 400	9.1	73	20.0
Trout	34 700	71 800	17.5	49	13.6
Great Lakes					
Nipigon	484 800	2 450 000	25.6	143	58.5
Superior*	8 223 600	21 000 000	180.4	403	148.7

1 sample·s^{-1}, precision of depth sensor ~0.05 m) that was lowered at a rate of ~0.5 m·s^{-1}. This instrument was calibrated on several occasions with a manual resistance thermometer accurate to 0.1°C. The planar thermocline depth is defined as that depth where the rate of change of temperature with depth is greatest (normally >1°C·m^{-1}).

The coefficient of eddy diffusivity, K_z, was estimated using Ward's (1977) equation

$$(2)\quad K_z = 4.9 \times 10^{-12} \frac{g\sqrt{A_0}}{N}$$

where g is the gravitational acceleration constant (9.81m·s^{-2}), A_0 is the lake surface area, and N is the Brunt-Väisälä frequency:

$$(3)\quad N = \sqrt{\frac{d\rho}{dz} \cdot \frac{g}{\rho}}$$

where ρ is the density of water. In oligotrophic Canadian Shield waters, ρ can be assumed to be solely a function of temperature (Quay et al. 1980) and we calculated it using Benson and Krause's (1980) equation

$$(4)\quad \rho = \exp(-0.589581 + 326.785/T - 45284.1/T^2)$$

where T is ^0K. Units throughout are metres and seconds, except for ρ which has units of grams per cubic centimetre.

Water chemistry depth profiles were determined twice: once at the beginning and again at the end of summer stratification (mid-June and late August, except in Trout Lake and Lake Nipigon, where corresponding temperature stratification conditions occurred in early July and mid-September); chemistry profiles were not measured on Orange Lake or Lake Superior. A PVC Van Dorn bottle was used to collect water samples,which were transported to the laboratory in polyethylene bottles precleaned with dilute HCl, followed by three rinses of distilled water,and then air-dried. The following forms of nitrogen (N), phosphorus (P),and silicon (Si) were measured: $NO_3^- + NO_2^-$; NO_2^- (which was below the limit of detection everywhere); NH_4^+; total dissolved N

TABLE 2. Early and late summer values (upper and lower rows, respectively) of thermocline depth (z_{th}); the ratio of the area of the lake at the depth of the thermocline to the surface area (A_z/A_0); the Brunt-Väisälä frequency (N); the eddy diffusivity (K_z); nutrient concentration gradients in the thermocline; and nutrient fluxes through the thermocline, expressed per unit area of lake surface.

	z_{th} (m)	A_z/A_0	N (s)	K_z ($m^2 \cdot s^{-1} \times 10^{-5}$)	Gradient ($\mu mol \cdot m^{-3} \cdot m^{-1}$)						Flux ($\mu mol \cdot m^{-2} \cdot d^{-1}$)					
					NO_3^-	TIN	TN	TDP	TP	SRSi	NO_3^-	TIN	TN	TDP	TP	SRSi
Lake 373	5.0	0.68	0.087	0.030	0	57	400	0	19	−427	0	1	7	0	0	−7
	7.0	0.62	0.097	0.027	0	95	619	11	22	−1317	0	1	9	0	0	−19
Green	5.0	0.69	0.054	0.083	286	1000	2000	0	81	−837	14	50	99	0	4	−41
	7.0	0.49	0.105	0.043	0	0	71	0	0	1175	0	0	1	0	0	22
Linge	6.5	0.50	0.045	0.285	0	0	−143	0	0	1187	0	0	−18	0	0	146
	8.5	0.40	0.084	0.152	48	48	−1286	−22	−43	5483	2	2	−67	−1	−2	287
Musclow	7.8	0.78	0.025	0.899	32	32	−325	0	−15	81	20	20	−196	0	−9	49
	9.0	0.74	0.078	0.289	357	357	286	0	−16	884	66	66	53	0	−3	164
Sydney	11.2	0.55	0.025	1.442	99	222	148	0	0	86	68	153	102	0	0	59
	12.0	0.53	0.039	0.940	300	300	−171	−6	−19	64	129	129	−73	−3	−8	28
Trout	14.1	0.38	0.042	2.127	145	145	−24	0	0	241	102	102	−17	0	0	169
	11.8	0.45	0.072	1.238	19	19	−545	6	0	1851	9	9	−261	3	0	886
Nipigon	13.3	0.79	0.043	7.767	235	21	−53	5	0	159	1236	112	−279	25	0	840
	11.9	0.81	0.049	6.877	276	276	210	0	−2	522	1327	1327	1009	0	−10	2509

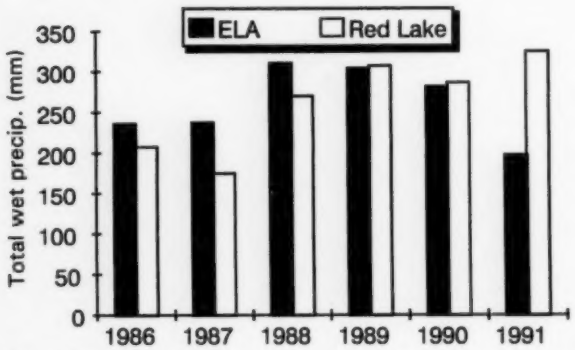


FIG. 1. Total wet precipitation received at the Experimental Lakes Area (ELA) field station and at Red Lake, Ontario, during the period June 1 – August 31.

(TDN); suspended particulate N (SPN); suspended particulate P (SPP); total dissolved P (TDP); and soluble reactive Si (SRSi). Total inorganic N (TIN = $NO_3^- + NO_2^- + NH_4^+$), total P (TP = TDP + SPP), and total N (TN = TDN + SPN) were obtained arithmetically. Orthophosphate (PO_4^{3-}) is undetectable in these waters (Stainton 1980).

Turbulence-mediated nutrient fluxes up through the thermocline (mass·$m^{-2} \cdot d^{-1}$) were multiplied by the ratio of the area of the lake at the depth of the thermocline (A_{th}) to the surface area of the lake (A_0) (Table 2); this renders them directly comparable with other fluxes to the mixed layer (precipitation, terrestrial runoff, and N_2-fixation) and to the nutrient requirements of phytoplankton, which were based on the rate of phytoplankton photosynthesis per square metre of lake surface, corrected for the diminution of lake volume with depth (Fee 1980).

Chemical concentrations were not measured in Orange Lake or Lake Superior; mixing fluxes thus cannot be calculated for these lakes directly. Mixing fluxes in Orange Lake were estimated by interpolating linearly (lake surface area being the independent variable) from those measured in Green and Linge Lakes. Because Lake Superior is the largest member of the size series, this method cannot be used and mixing fluxes are not available for this lake.

The N, P, and Si requirements of phytoplankton residing in the mixed layer were estimated by dividing the rate of PP (mol C·$m^{-2} \cdot d^{-1}$, daily average for the period June 1 – August 31, corrected for the diminution of lake volume with depth, Fee 1980; data summarized by Fee et al. 1992) by the ratios of the concentrations of these nutrients to the concentration of carbon (C) in suspended particulate matter. For example, the amount of P needed to match the C fixed in photosynthesis is

$$(5)\quad P_{required} = \frac{PP_{areal}}{C : P_{particulate}}.$$

Suspended C, N, and P were determined on integrated (0–3 m) water samples collected every 3 wk during the summer of 1990. Suspended Si samples were collected in the same way, but in 1991 and 1992; they were analyzed using the method of Paasche (1973) modified by digesting filters in NaOH for a longer period (2 h).

Bulk precipitation (rainfall plus accumulated dryfall) was collected after each significant rainfall event from a collector on the island in ELA Lake 240. Rainfall volume and chemical composition data collected there were assumed to apply to all the studied lakes; this is in agreement with the *Hydrological Atlas of Canada* (1978), which shows that the NOLSS and ELA areas (150 km apart) receive the same annual wet precipitation. In fact, similar total summer rainfall volumes fell at Red Lake, Ontario, which is near the center of the NOLSS study area, during this study (Fig. 1, average ratio for the 6 yr period = 1.04). According to the Hydrological Atlas, Lakes Nipigon and Superior receive about 30% more wet precipitation than the ELA and NOLSS regions.

Nutrient fluxes from terrestrial runoff were based on measurements made in the basin of ELA Lake 239, the long-term ELA reference lake A_0 = 56 ha, maximum depth (z_m) = 30 m, mean depth ($\bar{z}$) = 11 m, nominal water renewal time (τ_w) = ~6 yr. The volumes of streams entering this lake were measured continuously, and chemical concentrations

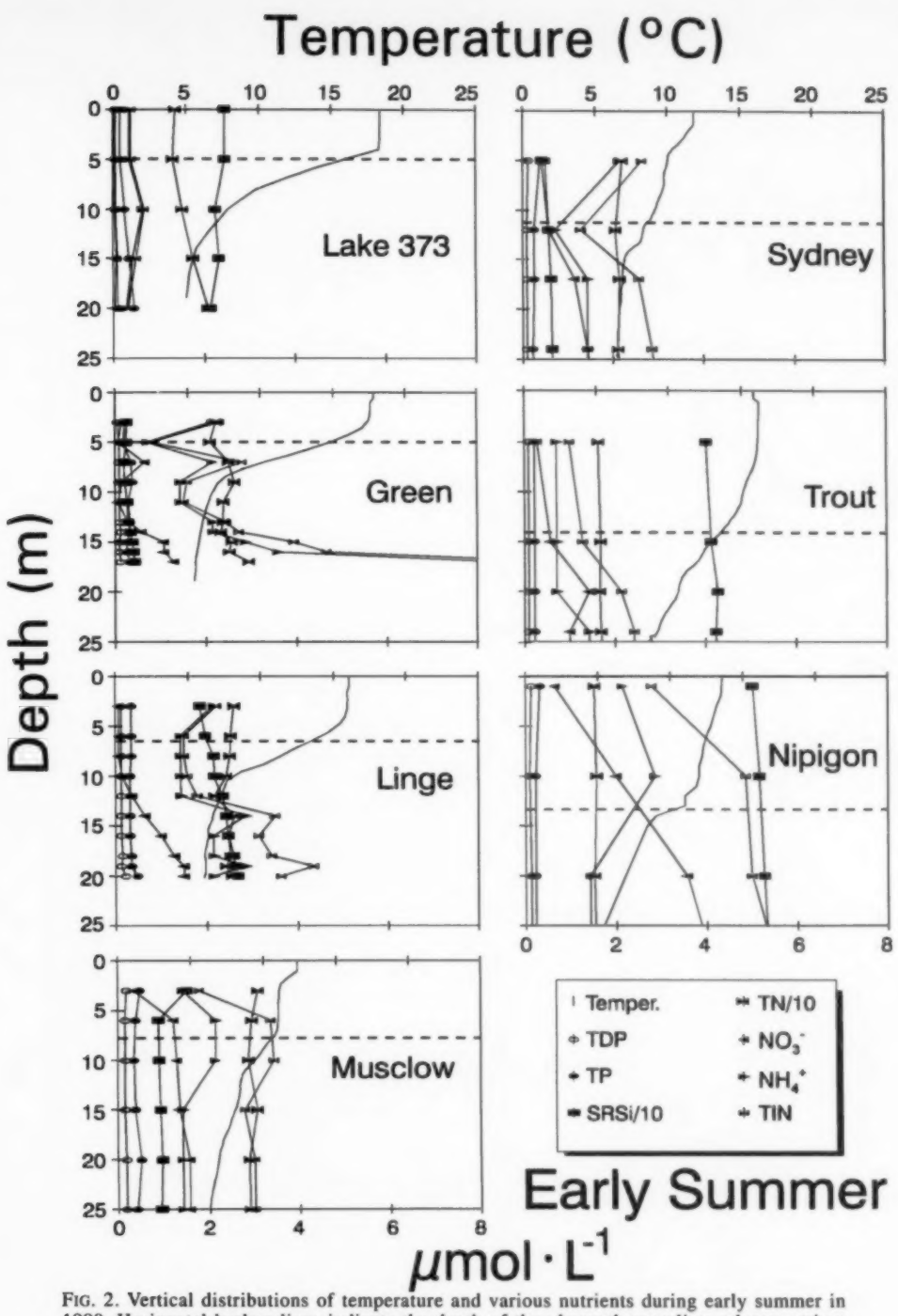


FIG. 2. Vertical distributions of temperature and various nutrients during early summer in 1990. Horizontal broken lines indicate the depth of the planar thermocline, where nutrient fluxes were calculated. To facilitate comparison with small lakes, and because concentrations did not change much at greater depths, only data from the top 25 m of the water column are shown for the deeper lakes. TN, total nitrogen; TP, total phosphorus; SRSi, soluble reactive silicon.

in these streams were measured at intervals of 1–2 wk. Fluxes of nutrients during the period June 1 – August 31 were calculated by summing the product of the total flow during each measurement interval times the chemical concentration at the end of the interval. Runoff from areas not drained by defined streams was estimated by multiplying

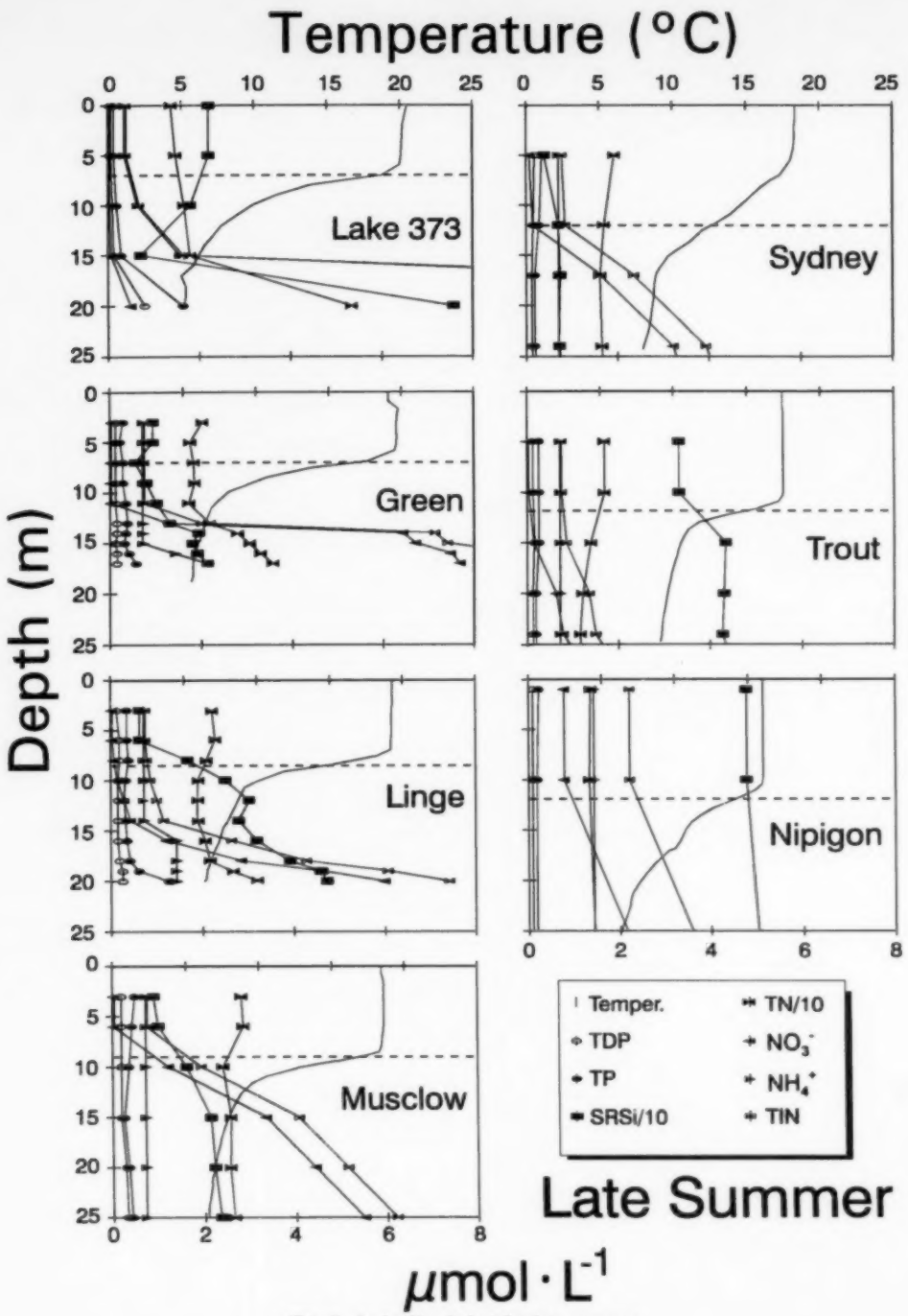


FIG. 3. As in Fig. 2, but for late summer.

the fluxes from the Lake 239 northwestern subbasin by the ratio of the total area not drained by streams to the area of the northwestern subbasin. These fluxes were applied to lakes in the size series by assuming constant nutrient yields per unit of drainage basin area. Lake 239 is a headwater lake, so this procedure probably overestimates fluxes to lakes larger than 100 ha, because all these basins contain wetlands and lakes with long residence times, which selectively retain P (Schindler et al. 1976; Fee and Hecky 1992).

The organic C content of profundal sediments was determined on the top 5 cm of cores taken from a deep-water station on each lake. Total C was determined by combustion

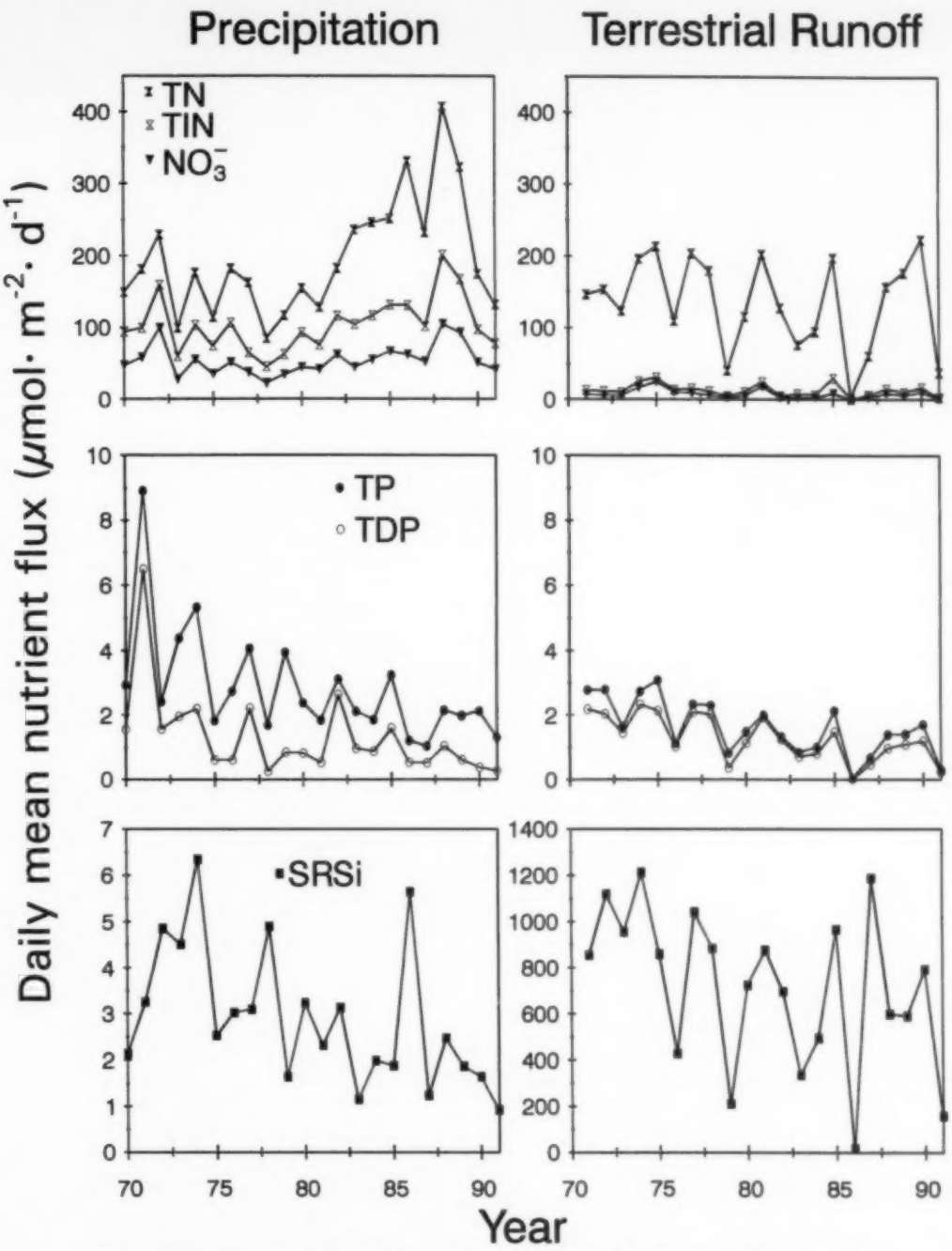


FIG. 4. Daily mean nutrient flux to the mixed layer of Lake 239 from precipitation and terrestrial runoff for the period June 1 – August 31. Note scale change for Si in rain versus terrestrial runoff. See text for definition of abbreviations.

of dried sediment in an oxygen–helium atmosphere at 950°C; CO_2 in the resulting gas mixture was determined on a Control Equipment Corp. Model 240-XA Elemental Analyzer (thermal conductivity detector). The concentration of inorganic C was determined by digesting 10 g of dried sediment in 10 mL of dilute sulfuric acid (pH ~4); this converted carbonates and bicarbonates to CO_2, which was purged from solution and detected on an O,I Corp. Model 700 TOC Analyzer (infrared detector). Organic C was calculated as the difference between total C and inorganic C.

N_2-fixation was measured on integrated (0–3 m) whole-water samples taken every 3 wk during the summers of

TABLE 3. Mixed-layer daily averages for the period June 1 – August 31 of phytoplankton photosynthesis, terrestrial runoff, mixing, and N_2-fixation. See text for definition of abbreviations.

	Phytoplankton photosynthesis ($\mu mol \cdot m^{-2} \cdot d^{-1}$)		Particulate ratios mol/mol			Phytoplankton requirements ($\mu mol \cdot m^{-2} \cdot d^{-1}$)					
						1990			7-yr min		
	1990	7-yr min	C/P	C/N	C/Si	N	P	Si	N	P	Si
Lake 373	7 393	5 765	430	13.7	18.0	540	17	411	421	13	320
Green	14 240	7 249	420	13.2	23.8	1080	34	598	550	17	304
Orange	16 852	11 837	364	11.3	13.2	1494	46	1273	1049	32	894
Linge	26 828	12 344	301	10.9	17.1	2457	89	1568	1130	41	721
Musclow	34 222	19 701	278	10.2	14.0	3362	123	2441	1935	71	1405
Sydney	19 697	14 090	274	13.7	13.0	1440	72	1515	1030	51	1084
Trout	21 424	14 615	292	14.3	10.9	1498	73	1960	1022	50	1337
Nipigon	29 309	23 529	205	9.6	7.3	3041	143	3998	2442	115	3210
Superior	13 055	13 055	365	10.4	9.6	1255	36	1358	1255	36	1358
Precipitation											

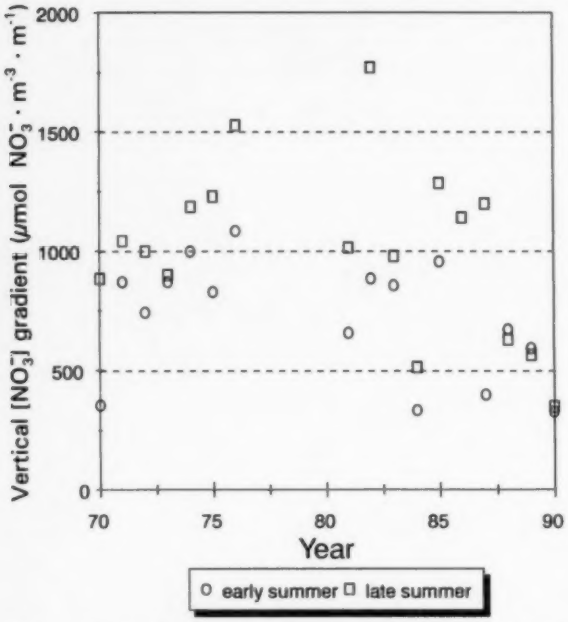


FIG. 5. Vertical gradient of nitrate concentrations in the thermocline of Lake 239 at the beginning and end of summer stratification.

1990 and 1991. Measurements were made with a modification of Flett et al.'s (1976) glass syringe incubation method (Hendzel et al. 1994). In situ N_2-fixation rates were calculated from acetylene production rates using Flett et al.'s (1976) average ratio of 1 mol of N_2 fixed for every 3 mol of ethylene produced. These were converted to daily areal rates by assuming that irradiances suitable for N_2-fixation at the measured rate occurred throughout the mixed layer for 10 h.

Results

The largest nutrient concentration gradients occurred deep in the hypolimnia of small lakes (top three panels in the left columns of Fig. 2 and 3); gradients were much smaller in larger lakes (right column of panels in Fig. 2 and 3). However, mixing fluxes through the thermocline depend only on concentration gradients at the depth of the thermocline (Equation (1)), and there was no obvious relationship between gradients at this depth and lake size (Table 2). Thus, lake-to-lake differences in the upward flux of individual nutrients through the thermocline depend almost entirely on K_z, which was more than two orders of magnitude greater in the largest lake (Nipigon) than in the smallest (ELA Lake 373) (Table 2). Fluxes increased progressively with lake size for those nutrients that increased in concentration with depth in the region of the thermocline (NO_3^-, TIN, and SRSi) but were nil for nutrients that had zero or negative gradients (TN, TDP, TP).

Over a 21-yr period, the summer mixed layer of ELA Lake 239 received similar amounts of TN and TP from precipitation and terrestrial runoff (Fig. 4). There was always much more TIN and NO_3^- in precipitation than in runoff, but runoff was by far the most important source of Si. In 1990, upward mixing through the thermocline was an important source of nutrients (compared with precipitation and runoff) only in lakes >1000 ha (Table 3). The amount of N supplied by N_2-fixation was much less than that supplied by precipitation and runoff except in intermediate-sized lakes; why higher N_2-fixation rates occurred in these lakes is unclear, because other fluxes of N to them were not unusually low. Interannually, fluxes from precipitation and terrestrial runoff varied by about the same amount as did nutrient concentration gradients in the thermocline of Lake 239 (Fig. 5); the coefficients of variation of NO_3^- in precipitation and of concentration gradients of NO_3^- in the Lake 239 thermocline were both 40%. Figure 5 also shows that in 1990 (the only year for which we have the chemistry depth profile data required to estimate vertical mixing fluxes in the NOLSS lakes) vertical concentration gradients in Lake 239 were unusually low. If interannual variations of chemical concentration gradients in Lake 239 also occur in larger lakes, then mixing fluxes would be about double those given in Table 2 in an average year, and up to three times greater in high years.

In 1990, fluxes of N and P to the mixed layer fell far short of phytoplankton requirements (Table 3 and left column of panels in Fig. 6), but the deficit of Si was slight. Minimizing nutrient requirements, by basing them on the lowest

ratios of nutrients in suspended particulate matter, phytoplankton nutrient requirements, and fluxes to the mixed layer from rain,

Flux from terrestrial runoff ($\mu mol \cdot m^{-2} \cdot d^{-1}$)												Flux from mixing ($\mu mol \cdot m^{-2} \cdot d^{-1}$)						N_2-fixation ($\mu mol \cdot m^{-2} \cdot d^{-1}$)
1990						20-yr max												
NO_3^-	TIN	TN	TDP	TP	SRSi	NO_3^-	TIN	TN	TDP	TP	SRSi	NO_3^-	TIN	TN	TDP	TP	SRSi	
3	5	71	0.4	0.5	252	8	10	71	0.7	1.0	385	0	1	8	0.1	0.3	−13.2	
4	7	94	0.5	0.7	334	10	13	94	1.0	1.3	512	7	25	50	0.0	2.0	−10.0	28
11	17	231	1.2	1.8	819	26	32	231	2.4	3.2	125							12
7	11	150	0.8	1.1	531	17	21	150	1.6	2.1	813	1	1	−42	−0.6	−1.1	216.5	104
24	39	525	2.8	4.0	1862	58	72	525	5.5	7.2	285	43	43	−72	0.0	−5.9	106.3	216
13	21	286	1.5	2.2	1015	32	39	286	3.0	3.9	155	98	141	14	−1.4	−4.2	43.4	36
3	5	73	0.4	0.6	260	8	10	73	0.8	1.0	399	56	56	−139	1.4	0.0	527.5	45
8	13	179	1.0	1.4	636	20	25	179	1.9	2.5	973	1281	720	365	12.7	−5.2	1674.4	
4	7	91	0.5	0.7	321	10	12	91	0.9	1.2	492							
52	98	175	0.4	2.1	1.6	105	201	407	6.5	8.9	6.4							

rate of areal PP observed in 7 yr in the NOLSS lakes, and maximizing nutrient supplies, by using the maximum precipitation and terrestrial runoff fluxes observed in the 20-yr Lake 239 record, the maximum rate of N_2-fixation observed in 2 yr in the NOLSS lakes, and three times the 1990 vertical mixing fluxes (as suggested at the end of the previous paragraph), did not substantially alter this picture except in the smallest lakes, where supplies of N and P approximately matched requirements (Table 3 and right column of panels in Fig. 6).

Discussion

Turbulent mixing through the thermocline, the only nutrient flux to the mixed layer that is explicitly dependent on lake size, supplied less TN and TP than did those fluxes that are independent of lake size (precipitation, terrestrial runoff, N_2-fixation; Fig. 6). Mixing supplied more of some forms of N (NO_3^- and TIN) and of SRSi in larger than in smaller lakes (Table 3), but terrestrial runoff more than made up for the SRSi that turbulence failed to supply in small lakes. Thus, the only mixing fluxes of potential ecological importance are of NO_3^- and TIN. Although N plays an important role in determining phytoplankton community composition (Schindler 1977), it rarely limits algal biomass in unperturbed Canadian Shield lakes (Hecky and Kilham 1988). We, therefore, conclude that the turbulence-mediated upward flux of nutrients through the summer thermocline was an insignificant component of mixed-layer nutrient budgets in all sizes of Canadian Shield lakes in 1990.

We did not measure concentrations of PO_4^{3-}, the form of P most readily assimilated by phytoplankton, because standard chemical methods for measuring it always overestimate actual concentrations in Canadian Shield lakes (Stainton 1980). Moreover, when special radiochemical methods have been used to measure it, concentrations in these lakes were always minute (<0.003 $\mu mol \cdot L^{-1}$; Levine and Schindler 1980). Nevertheless, if PO_4^{3-} did increase in concentration with depth in the thermoclines of the lakes we studied, we may have missed an important source of this critical element. We obtained an upper bound on the magnitude of this flux by assuming that concentrations increase from 0 in the mixed layer to the highest summer values ever measured in the hypolimnia of unperturbed northwestern Ontario Canadian Shield lakes (0.003 $\mu mol \cdot L^{-1}$; Levine and Schindler, 1980) over a distance of 1 m in all the lakes. These extremely generous assumptions yield upward (mixing) fluxes of P on the order of 0.002 $\mu mol \cdot m^{-2} \cdot d^{-1}$, which amounts to only ~0.001% of the amount of P that phytoplankton living in the mixed layer require. We thus confidently conclude that the upward flux of PO_4^{3-} through the thermocline is insignificant in Canadian Shield lakes.

None of the foregoing conclusions depend critically on our use of Equation (2) to estimate K_z, which is a statistical fit to the results of Mortimer (1941), Jassby and Powell (1975), Hutchinson (1957), Hesslein and Quay (1973), and Ward (1977). Two of these papers (Mortimer's and Hutchinson's), in turn, summarize results from many other independent studies. A possible objection to these results, however, is that with one exception they are all based on measurements of the rate at which heat moved downward through the thermocline. The exception was Hesslein and Quay (1973), who found that in a very small, deep lake (ELA Lake 227; A_0 = 5 ha, z_m = 10 m) K_z as determined by measuring the transport of a dissolved material (radon gas) was much smaller than K_z as determined by measuring the transport of heat. This happened because turbulence was so low that transport was almost entirely the result of molecular diffusion, and heat has a higher coefficient of molecular conductivity than radon gas. Because all of our lakes are much larger than Lake 227, they have K_z values substantially greater than the molecular conductivity of heat, and this cannot be a problem here. Moreover, if K_z were smaller than the values we derived from Equation (2), vertical fluxes would be even smaller than those we calculated, which we have already concluded to be insignificant. Finally, because concentration gradients of all forms of P in the region of the thermocline were negligible, our conclusion that vertical fluxes of this critical element were nil in all lake sizes is completely independent of K_z.

Figure 6 shows that phytoplankton living in the mixed layer required much more P and N than all of the fluxes measured in 1990. The deficit of supply relative to demand was notably greater for P than for N, further confirming that P is the most limiting nutrient in Canadian Shield lakes (Schindler 1977, 1988; Fee 1979; Hecky and Kilham 1988; Levine and Schindler 1992; Hecky et al. 1993; S. Guildford and L. Hendzel, unpublished data). Some might object

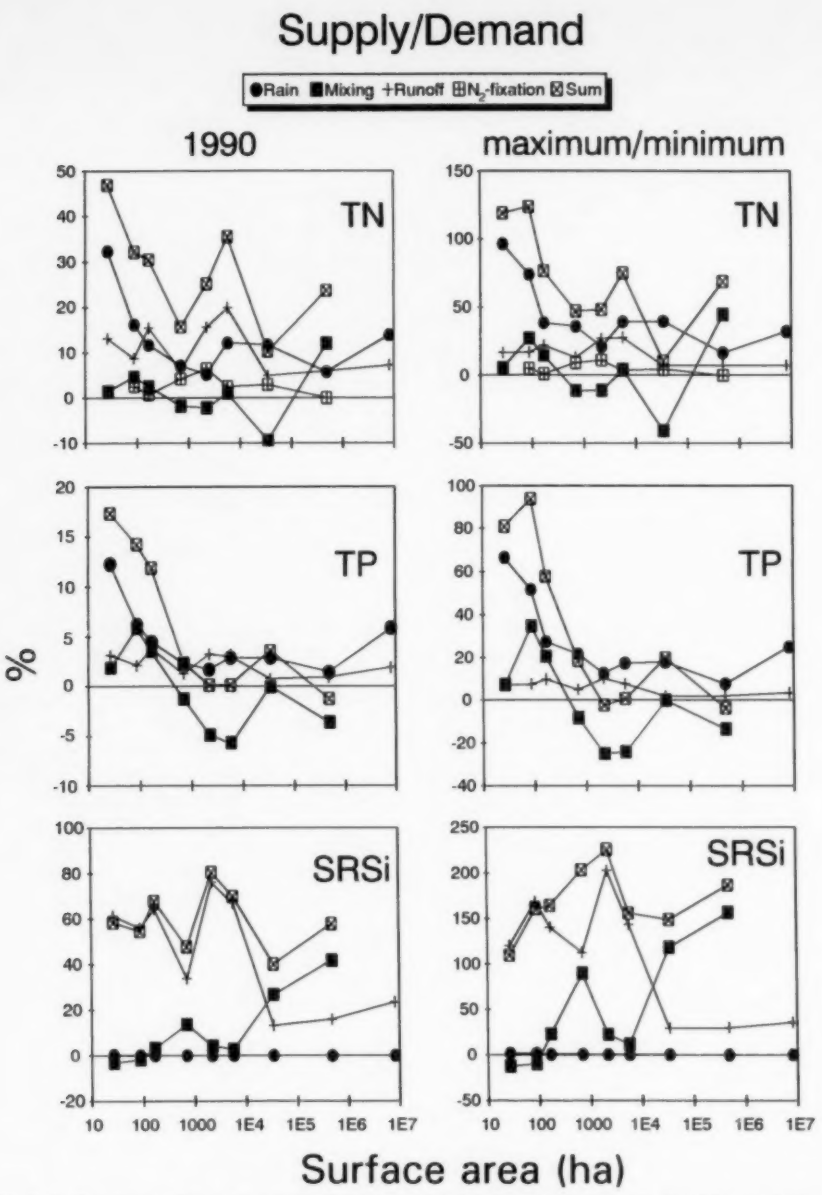


FIG. 6. Left column of panels: percentage of physiological requirements of mixed-layer phytoplankton that measured nutrient fluxes supplied in 1990. Right column of panels: same, but based on conservatively high estimates of nutrient supply (the 21-yr maximum flux from precipitation and terrestrial runoff, the 2-yr maximum rate of N_2-fixation, and three times the vertical mixing flux measured in 1990) and conservatively low estimates of phytoplankton nutrient requirements (the minimum rate of phytoplankton photosynthesis observed in 7 yr of study).

that allochthonous materials with elemental compositions very different from algae could be an important fraction of particulate matter; if so, our use of nutrient ratios in seston to estimate phytoplankton nutrient requirements from PP would be invalid. But Hecky et al. (1993) concluded that this was not a significant problem in Canadian Shield lakes with water residence times longer than a few months. Moreover, basing estimates of algal nutrient requirements on the Redfield ratios (106 for C/P and 6.6 for C/N; Redfield et al. 1963), which are widely accepted as the elemental composition of average algal cells, increases the gap between supply and demand because the C/P and C/N ratios of particles in our lakes were uniformly greater than the Redfield ratios (Table 3). Thus, our use of atomic ratios in particulate matter to estimate the nutrient requirements is, if anything, conservative.

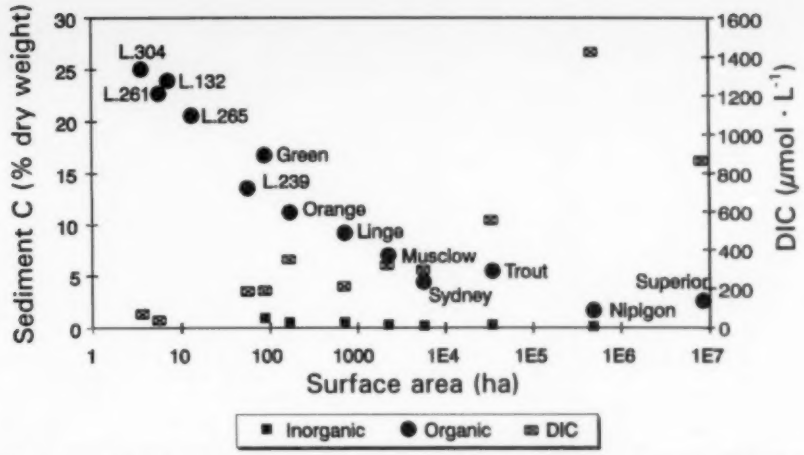


FIG. 7. June–August mean dissolved inorganic C (DIC) concentrations in the mixed layer and C content of profundal sediments in northwestern Ontario Canadian Shield lakes.

Another possible problem with our approach is that we assume that Fee et al.'s (1992) ^{14}C-based PP values estimate daily net C fixation into particles. We emphasize that our use of the term "net" is distinct from another common use of this term, i.e., the amount of material exported from the primary trophic level during an entire growing season (stored in sediments, flushed out of the lake, or converted into the flesh of higher trophic levels). We make no assumption about what happens to particles over periods longer than a day. Bower et al. (1987) showed that in an ELA whole-lake ^{14}C experiment, Fee et al.'s (1992) PP method closely approximated net daily incorporation of C into particles; all losses of ^{14}C from particles occurred at night, and these losses averaged only 8% of the daytime rate of incorporation of inorganic C into particulate matter (range 3–17%, $n = 13$). Essentially, we explicitly ignore this small and variable correction, and assume that the ^{14}C method used by Fee et al. (1992) yields estimates of daily net particulate C fixation; Peterson (1978) reported that this is true for rapidly growing algal cultures.

The final critical basic assumption for our analysis is that all major nutrient fluxes to the mixed layer were measured. One potential nutrient source that we did not measure is that from epilimnion sediments. However, studies at ELA have repeatedly demonstrated that epilimnion sediments return little or no P to the water column (^{32}P measurements: Schindler et al. 1975; Levine et al. 1986; mass balance calculations: Schindler et al. 1973, 1987; Levine and Schindler 1989; porewater gradient measurements: Schindler et al. 1977; L. Hendzel, unpublished data). Levine and Schindler (1989) did find that littoral sediments supplied N to the mixed layer, but as mentioned above, N rarely limits phytoplankton biomass in Canadian Shield lakes. Moreover, Levine and Schindler (1992) showed that the N returned to the water column from epilimnetic sediments was almost entirely derived from materials recently deposited at the sediment–water interface, rather than from deep within the sediment itself; in our view, this constitutes nutrient recycling within the mixed layer.

We thus conclude that Fig. 6 can be accepted at face value, and that fluxes of N and P to the mixed layer were a small fraction of the physiological requirements of phytoplankton in 1990. Indeed, these fluxes would be capable of meeting phytoplankton needs only in small lakes and if the most generous assumptions about supply and demand are made. The major implication is that recycling within the mixed layer must be the major source of N and P for algae living there. This is scarcely a new or surprising conclusion. Harrison (1980, and see references therein) showed that external inputs of N, P, and Si to the sea could account for <1% of the amounts required by phytoplankton, and he concluded that recycling supplied the remainder. In fresh water, Levine and Schindler (1980) found that in an unfertilized, stratified ELA lake (Lake 302S; $A_0 = 10.9$ ha, $z_m = 10.6$ m) an average P atom recycled through epilimnetic seston 17 times prior to being lost from the mixed layer, and Levine et al. (1986, p. 376) stated that "... the predominant source of phosphate for phytoplankton in the epilimnion is not external supply, but recycling." This result has been corroborated by so many independent studies (see Planas and Hecky 1984, and references therein) that it would have been extremely surprising if our results contradicted it.

Figure 6 illustrates what may be our single most important result, viz., the fraction of phytoplankton nutrient requirements accounted for by all estimated fluxes to the mixed layer systematically decreases with increasing lake size. That is, nutrient recycling within the mixed layer supplies a progressively increasing fraction of phytoplankton nutrient requirements as lake size increases. This is logical, because both the intensity of turbulence within the mixed layer and the thickness of the mixed layer increase with lake size. As a consequence, mixed-layer particle residence times increase with lake size; this increases the probability that particle-bound nutrients will be recycled within the mixed layer rather than being lost to the sediments. A lower bound on the magnitude of this effect can be derived using Hesslein et al.'s (1980) value of 0.18 $m \cdot d^{-1}$ for the settling rate of particles from the mixed layer of ELA Lake 224 ($A_0 = 25.9$ ha, $z_m = 27$ m). Applying this figure to all lake sizes, it would take 33 d for settling to remove all particles from the mixed layer of ELA Lake 373 ($z_{th} = 6$ m) compared with 72 d in Trout Lake ($z_{th} = 13$ m). However, because large lakes have

much more turbulent mixed layers than small ones, the actual difference in particle residence times in large versus small lakes is undoubtedly even greater.

The percent organic C in deep-water sediments declines in a strikingly regular fashion with increasing lake size (Fig. 7). This result strongly supports our conclusion that the rate of nutrient recycling within the mixed layer increases with increasing lake size.The longer that particles are retained in the mixed layer, the more likely it is that the C they contain will be respired back to CO_2 and lost to the atmosphere rather than falling through the thermocline and accumulating in deep-water sediments. We do not believe that recycling is the only process responsible for producing this pattern. Indeed, such regularity is probably the product of many processes acting in concert (e.g., longer retention in the mixed layer, increasing total depth of the water column, decreasing terrestrial influence, etc.). Nevertheless, it is fully consonant with our conclusion that large lakes recycle nutrients more efficiently than small ones.

The greater efficiency of nutrient recycling in the mixed layer in large than in small lakes has important implications for Fee's (1979) theory that the rate of nutrient recycling is a function of basin morphometry. He found that in small ELA lakes, the area of epilimnion sediments (A_e) divided by the volume of the epilimnion (V_e) was strongly correlated with rates of volumetric PP. He demonstrated that, if all other factors are equal, A_e/V_e is mathematically equivalent to the probability of retention of particles in the mixed layer and thus parameterized the rate of nutrient recycling. He cautioned that this might not be true in larger lakes, where processes that are negligible in small lakes could affect nutrient recycling. Our results bear out this prediction; as lakes increase in size, the increasing intensity of turbulence within the mixed layer and the increasing thickness of the mixed layer both retard sedimentation losses through the thermocline, thereby increasing mixed layer particle residence time. Consequently, a large lake with a low A_e/V_e value and a small lake with a high A_e/V_e value could have the same mixed layer particle residence times and similar rates of nutrient recycling. An important corollary is that large and small lakes with similar A_e/V_e values should respond differently to the same external P loading. Productivity should be higher in the large lake because of its higher rate of nutrient recycling. These results lend strong support to Margalef's (1974) theory that physical energy levels directly control food-web structures and the biogeochemical characteristics of water bodies.

The largest nutrient concentration gradients occurred deep in the water column of small lakes (Fig. 2 and 3); in contrast, large lakes had relatively well-mixed hypolimnia with maximum gradients at or just below the thermocline. This difference is probably the result of several processes: (1) Internal waves, which are the primary source of hypolimnetic turbulence, are significant only in lakes with surface areas >1000 ha (Boyce 1974); thus, in small lakes, nutrients from particles remineralized near the bottom of the water column move upward very slowly compared with larger lakes. (2) Sediment focussing is very important in small lakes (Anderson et al. 1987) and causes particles that fall through the thermocline to move rapidly to great depths. (3) Because small lakes have shallow mixed layers, significant quantities of light penetrate below their thermoclines (Fee et al. 1991), permitting large algal populations to develop deep in their water columns (Fee 1976). These algal populations intercept nutrients diffusing up from below and prevent them from reaching the thermocline.

Schindler and Nighswander (1970) and Bayley et al. (1992) reported that precipitation was the major source of N and P to Canadian Shield lakes.However, their conclusion was based on results obtained from the study of quite small lakes. Our results (Fig. 6) indicate that this does not apply to Canadian Shield lakes >300 ha, where fluxes of N and P from terrestrial runoff and precipitation were very similar in magnitude.

Unlike N and P, there was virtually no Si in precipitation, and mixing supplied substantial quantities of this nutrient only in very large lakes (Fig. 6). However, terrestrial runoff of Si was large, particularly in small and midsized lakes, and the sum of all the fluxes that we measured apparently match phytoplankton requirements. There must, therefore, be some reason, other than a lack of supply, for why diatoms are unimportant components of the summer phytoplankton community in small, stratified Canadian Shield lakes (Kling and Holmgren 1972; Findlay and Kasian 1990). Again, the most likely explanation is based on the low mixed-layer turbulence and shallow mixed-layer depths in small lakes. Theoretically, the higher specific gravity of diatoms gives them a selective advantage over nonsinking or weakly motile competitors because by sinking they increase the rate at which they contact dissolved nutrients (by thinning the nutrient-depleted boundary layer that surrounds them: Hutchinson 1967; Margalef 1974; Titman and Kilham 1976). This strategy works well in large lakes, where high turbulence and deep mixed layers keep cells from being rapidly lost by sedimentation through the thermocline. Diatoms are also well represented in small, unstratified lakes, which lack a hypolimnion sedimentation trap altogether (Kling and Holmgren 1972). However, this strategy apparently fails in small, stratified lakes where shallow mixed layers and relatively stable water columns lead to rapid removal of sinking cells from the mixed layer.

Conclusion

The increasing intensity of turbulence with lake size acted in concert with positive concentration gradients of NO_3^-, TDN, and SRSi in the region of the thermocline to result in more of these nutrients being transported upwards through the thermoclines in large than in small lakes (Table 2). These nutrients, however, rarely limit phytoplankton growth in Canadian Shield lakes. Because concentration gradients of P, the nutrient that does limit algal growth in Canadian Shield lakes, were nil in the region of the thermocline in all of these lakes (Fig. 2 and 3; Table 2), upward fluxes of P were essentially zero in all lake sizes.

Our results support Fee et al.'s (1992) hypothesis that the increasing intensity of turbulence with lake size stimulates PP. It does this by acting in concert with the increasing depth of the mixed layer to cause particles to be retained in the mixed layer longer, thus increasing the probability that nutrients will be recycled within the mixed layer rather than lost to the sediments. Our results do not, however, rule out the possibility that the greater rates of volumetric PP in midsized lakes reported by Fee et al. (1992) are caused by lake-to-lake differences of external P loading. That is, although our results show that, all other things being equal,

higher turbulence and thicker mixed layers enhance nutrient recycling and lead to higher rates of areal PP in larger lakes, the approach we have taken of using runoff and precipitation data measured in the basin of one small ELA lake to estimate P loading in all the other lakes has inherent inaccuracies (Fee and Hecky 1992). External P loading within this lake-size series could vary enough to explain the observed differences of volumetric PP. Nevertheless, Fee et al. (1992) showed that it is unlikely that areal PP, which theoretically sets potential yields of higher trophic levels, is the result of lake-to-lake differences in external P loading.

Our main conclusion, that the probability of regeneration of nutrients within the mixed layer increases with lake size, has an important corollary: external nutrient loads should be converted into higher trophic levels, including especially valued organisms such as fish, more efficiently in large than in small lakes. This prediction is in harmony with Nixon's (1988) conclusion that the greatest standing crops of benthos and highest fish yields come from the most energetic marine environments. He further noted that, as we found in large lakes, sediments from these highly productive regions contained less C than did sediments from less energetic environments. His interpretation of these observations was also the same as ours, viz., that energetic mixed layers recycle nutrients more efficiently than less energetic ones.

Acknowledgments

A Natural Sciences and Engineering Research Council of Canada strategic grant to C. Kelly and J. Rudd supported collection of the water chemistry depth profile samples. We thank C. Anema for overseeing most aspects of the field work, and J. Boughen for suspended silica determinations. R. Hesslein, P. Campbell, and D. Schindler commented helpfully on the manuscript.

References

Anderson, R.F., S.L. Schiff, and R.H. Hesslein. 1987. Determining sediment accumulation and mixing rates using ^{210}Pb, ^{137}Cs, and other tracers: problems due to postdepositional mobility or coring artifacts. Can. J. Fish. Aquat. Sci. 44(Suppl. 1): 231–250.

Bayley, S.E., D.W. Schindler, K.G. Beaty, B.R. Parker, and M.P. Stainton. 1992. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorus. Can. J. Fish. Aquat. Sci. 49: 584–596.

Benson, B.B., and D. Krause, Jr. 1980. The concentration and isotopic fractionation of gasses dissolved in freshwater in equilibrium with the atmosphere. 1. Oxygen. Limnol. Oceanogr. 25: 662–671.

Bower, P.M., C.A. Kelly, E.J. Fee, J.A. Shearer, D. R. DeClercq, and D.W. Schindler. 1987. Simultaneous measurement of primary production by whole-lake and bottle radiocarbon additions. Limnol. Oceanogr. 32: 299–312.

Boyce, F.M. 1974. Some aspects of Great Lakes physics of importance to biological and chemical processes. J. Fish. Res. Board Can. 31: 689–730.

Fee, E.J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: implications for primary production estimates. Limnol. Oceanogr. 21: 767–783.

Fee, E.J. 1979. A relation between lake morphometry and primary production and its use in interpreting whole-lake eutrophication experiments. Limnol. Oceanogr. 24: 401–416.

Fee, E.J. 1980. Important factors for estimating annual phytoplankton production in the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. 37: 513–522.

Fee, E.J., and R.E. Hecky. 1992. Introduction to the Northwest Ontario Lake Size Series (NOLSS). Can. J. Fish. Aquat. Sci. 49: 2434–2444.

Fee, E.J., R.E. Hecky, M.P. Stainton, P. Sandberg, L.L. Hendzel, S.J. Guildford, H.J. Kling, G.K. McCullough, C. Anema, and A. Salki. 1989. Lake variability and climate research in Northwest Ontario: study design and 1985–1986 data from the Red Lake District. Can. Tech. Rep. Fish. Aquat. Sci. 1662: 39 p.

Fee, E.J., E.U. Schindler, J.A. Shearer, E.R. DeBruyn, and D.R. DeClercq. 1991. Light attenuation in the mixed-layer of lakes in the Experimental Lakes Area, 1969–1990 data. Can. Data Rep. Fish. Aquat. Sci. 850: 59 p.

Fee, E.J., J.A. Shearer, E.R. DeBruyn, and E.U. Schindler. 1992. Effects of lake size on phytoplankton photosynthesis. Can. J. Fish. Aquat. Sci. 49: 2445–2459.

Findlay, D.L., and S.E.M. Kasian. 1990. Phytoplankton communities of lakes experimentally acidified with sulfuric and nitric acids. Can. J. Fish. Aquat. Sci. 47: 1378–1386.

Flett, R.J., R.D. Hamilton, and N.E.R. Campbell. 1976. Aquatic acetylene reduction techniques. Solutions to several problems. Can. J. Microbiol. 22: 43–51.

Harrison, W.G. 1980. Nutrient regeneration and primary production in the sea, p. 433–460. *In* P.G. Falkowski [ed.] Brookhaven Symposium in Biology, No. 31. Environ. Sci. Res. 19.

Hecky, R.E., P. Campbell, and L.L. Hendzel. 1993. The stoichiometry of carbon, nitrogen, and phosphorus in particulate matter of lakes and oceans. Limnol. Oceanogr. 38: 709–724.

Hecky, R.E., and P. Kilham. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. Limnol. Oceanogr. 33(4, part 2): 796–822.

Hendzel, L.L., R.E. Hecky, and D.L. Findlay. 1994. Recent changes of N_2-fixation in Lake 227 in response to reduction of the N:P loading ratio. Can. J. Fish. Aquat. Sci. 51: 2247–2253.

Hesslein, R., and P. Quay. 1973. Vertical eddy diffusion studies in the thermocline of a small stratified lake. J. Fish. Res. Board Can. 30: 1491–1500.

Hesslein, R.H., W.S. Broecker, and D.W. Schindler. 1980. Fates of metal radiotracers added to a whole lake: sediment–water interactions. Can. J. Fish. Aquat. Sci. 37: 378–386.

Hutchinson, G.E. 1957. A treatise on limnology. Vol. 1. Geography, physics, and chemistry. John Wiley & Sons, New York, N.Y. 1015 p.

Hutchinson, G.E. 1967. A treatise on limnology. Vol. 2. Introduction to lake biology and the limnoplankton. John Wiley & Sons, New York, N.Y. 1115 p.

Jassby, A.D., and T. Powell. 1975. Vertical patterns of eddy diffusion during stratification in Castle Lake, California. Limnol. Oceanogr. 20: 530–543.

Johnson, W.E., and J.R. Vallentyne. 1971. Rationale, background, and development of experimental lakes studies in northwestern Ontario. J. Fish. Res. Board Can. 28: 123–128.

Kling, H.J., and S.K. Holmgren. 1972. Species composition and seasonal distribution of phytoplankton in the Experimental Lakes Area, northwestern Ontario. Can. Fish. Mar. Serv. Tech. Rep. 337: 5 p.

Levine, S.N., and D.W. Schindler. 1980. Radiochemical analysis of orthophosphate concentrations and seasonal changes in the flux of orthophosphate to seston in two Canadian Shield lakes. Can. J. Fish. Aquat. Sci. 37: 479–487.

Levine, S.N., and D.W. Schindler. 1989. Phosphorus, nitrogen, and carbon dynamics of Lake 303 during recovery from eutrophication. Can. J. Fish. Aquat. Sci. 46: 2–10.

Levine, S.N., and D.W. Schindler. 1992. Modification of the N:P ratio in lakes by in situ processes. Limnol. Oceanogr. 37: 917–935.

Levine, S.N., M.P. Stainton, and D.W. Schindler. 1986. A radiotracer study of phosphorus cycling in a eutrophic Canadian Shield lake, Lake 227, northwestern Ontario. Can. J. Fish. Aquat. Sci. 43: 366–378.

Margalef, R. 1974. Ecología. Omega, Barcelona. 951 p.

Mortimer, C.H. 1941. The exchange of dissolved substances between mud and water in lakes. J. Ecol. 30: 147–201.

Nixon, S.W. 1988. Physical energy inputs and the comparative ecology of lake and marine ecosystems. Limnol. Oceanogr. 33: 1005–1025.

Paasche, E. 1973. Silicon and the ecology of marine plankton diatoms. I. *Thalassiosira pseudonana* growth in a chemostat with silicate as a limiting nutrient. Mar. Biol. 19: 117–126.

Peterson, B.J. 1978. Radiocarbon uptake: its relation to net particulate carbon production. Limnol. Oceanogr. 23: 179–184.

Planas, D., and R.E. Hecky. 1984. Comparison of phosphorus turnover times in northern Manitoba reservoirs with lakes of the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. 41: 605–612.

Quay, P.D., W.S. Broecker, R.H. Hesslein, and D.W. Schindler. 1980. Vertical diffusion rates determined by tritium tracer experiments in the thermocline and hypolimnion of two lakes. Limnol. Oceanogr. 25: 201–218.

REDFIELD, A.C., B.H. KETCHUM, AND F.A. RICHARDS. 1963. The influence of organisms on the composition of sea water, p. 26–77. *In* M.N. Hill [ed.] The sea. Wiley-Interscience, New York N.Y.

SCHINDLER, D.W. 1977. Evolution of phosphorus limitation in lakes: natural mechanisms compensate for deficiencies of nitrogen and carbon in eutrophied lakes. Science (Wash., DC) 195: 260–262.

SCHINDLER, D.W. 1988. Experimental studies of chemical stressors on whole lake ecosystems. Edgardo Baldi memorial lecture. Int. Ver. Theor. Angew. Limnol. Verh. 23: 11–41.

SCHINDLER, D.W., R.H. HESSLEIN, AND G. KIPPHUT. 1977. Interactions between sediments and overlying waters in an experimentally-eutrophied Precambrian Shield Lake, p. 235–243. *In* H.L. Golterman [ed.] Interactions between sediments and freshwater. W. Junk, The Hague.

SCHINDLER, D.W., R.H. HESSLEIN, AND M.A. TURNER. 1987. Exchange of nutrients between sediments and water after 15 years of experimental eutrophication. Can. J. Fish. Aquat. Sci. 44(Suppl. 1): 26–33.

SCHINDLER, D.W., H. KLING, R.V. SCHMIDT, J. PROKOPOWICH, V.E. FROST, R.A. REID, AND M. CAPEL. 1973. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, 1972. J. Fish. Res. Board Can. 30: 1415–1440.

SCHINDLER, D.W., D.R.S. LEAN, AND E.J. FEE. 1975. Nutrient cycling in freshwater ecosystems, p. 96–105. *In* D.R. Reichle [ed.] Productivity of world ecosystems. U.S. National Academy of Sciences, Washington, DC.

SCHINDLER, D.W., R.W. NEWBURY, K.G. BEATY, AND P. CAMPBELL. 1976. Natural water and chemical budgets for a small Precambrian lake basin in central Canada. J. Fish. Res. Board Can. 33: 2526–2543.

SCHINDLER, D.W., AND J.E. NIGHSWANDER. 1970. Nutrient supply and primary production in Clear Lake, eastern Ontario. J. Fish. Res. Board Can. 17: 2009–2036.

STAINTON, M.P. 1980. Errors in molybdenum blue methods for determining orthophosphate in fresh water. Can. J. Fish. Aquat. Sci. 37: 472–478.

STAINTON, M.P., M.J. CAPEL, AND F.A.J. ARMSTRONG. 1977. The chemical analysis of fresh water. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25: 180 p.

TITMAN, D., AND P. KILHAM. 1976. Sinking in freshwater phytoplankton: some ecological implications of cell nutrient status and physical mixing processes. Limnol. Oceanogr. 21: 409–417.

WARD, P.R.B. 1977. Diffusion in lake hypolimnia, p. 102–110. *In* Proceedings 17th Congress of the International Association for Hydraulic Research, August 15–19, 1977, Baden–Baden, Pap. A88.

Effects of Lake Size on Phytoplankton Nutrient Status[1]

S.J. Guildford, L.L. Hendzel, H.J. Kling, and E.J. Fee

Department of Fisheries and Oceans, Central and Arctic Region, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

G.G.C. Robinson

Department of Botany, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

and R.E. Hecky and S.E.M. Kasian

Department of Fisheries and Oceans, Central and Arctic Region, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Guildford, S.J., L.L. Hendzel, H.J. Kling, E.J. Fee, G.G.C. Robinson, R.E. Hecky, and S.E.M. Kasian. 1994. Effects of lake size on phytoplankton nutrient status. Can. J. Fish. Aquat. Sci. 51: 2769–2783.

Phytoplankton nutrient status measurements (C/P, C/N, C/chlorophyll, N/P, alkaline phosphatase activity, and N debt) were measured for 6 yr in seven remote Canadian Shield lakes. Lakes Nipigon and Superior were also studied for 2 yr. These lakes varied in surface area from 29 to 8.223×10^6 ha, they all stratified fully during the summer and had water renewal times >5 yr. All lakes were severely P deficient; however, the large lakes (>2000 ha) were consistently less P deficient than small lakes. A growth-rate indicator (photosynthesis normalized to particulate C) agreed with nutrient status indicators, in that small lakes had lower rates than large lakes. Total P was a good predictor of chlorophyll, but factors related to lake size (temperature and mixed depth) were equally good or better predictors of nutrient status. Decreasing mean water column light intensity could not explain the lower P deficiency of large lakes. The deeper, more energetic mixed layers in large lakes apparently cause P to be recycled more efficiently. Extrapolation of observations or experimental results from small to large lakes requires recognition that phytoplankton in large lakes are less nutrient deficient and may have higher growth rates.

Les conditions nutritives du phytoplancton (C/P, C/N, C/chlorophylle, N/P, activité de la phosphatase alcaline, déficit en N) ont été mesurées durant 6 ans dans sept lacs éloignés du Bouclier canadien. Les lacs Nipigon et Supérieur ont également été étudiés durant 2 ans. Les lacs avaient des superficies variant entre 29 et 8223×10^6 ha, ils présentaient une stratification complète durant l'été et leurs eaux se renouvelaient en plus de 5 ans. Les concentrations de P étaient très faibles dans tous les lacs; cependant, elles étaient plus fortes dans tous les grands lacs (>2000 ha). Le taux de photosynthèse normalisée en fonction du C particulaire, utilisé comme indicateur de croissance, entrait en corrélation avec les indicateurs de conditions nutritives, les taux de photosynthèse dans les petits lacs étant inférieurs à ceux mesurés dans les grands lacs. Le P total constituait un bon paramètre de prévision pour la chlorophylle, mais les facteurs liés à la taille des lacs (température et profondeur de la couche de mélange) permettaient une prévision des conditions nutritives aussi bon ou même meilleure. L'intensité lumineuse décroissante dans la zone moyenne de la colonne d'eau ne peut expliquer le fait que le manque de P est moins marqué dans les grands lacs. Dans cer derniers, le fait que la couche de mélange soit plus profonde et plus agitée entraînerait un meilleur recyclage du P. L'extrapolation des observations ou des résultats expérimentaux obtenus dans les lacs de petite à grande taille exige qu'on reconnaisse que le phytoplancton des grands lacs manque moins d'éléments nutritifs et peut montrer des taux de croissance plus élevés.

Received February 14, 1994
Accepted July 12, 1994
(J12275)

Reçu le 14 février 1994
Accepté le 12 juillet 1994

Phytoplankton nutrient status measurements have a variety of uses. First, they indicate the specific nutrient or nutrients controlling phytoplankton growth (Healey and Hendzel 1980; Hecky and Kilham 1988; Suttle et al. 1991). Second, they are essential for managing water quality of lakes and controlling nuisance algae (Schindler 1977; Lean 1987; Lohman and Priscu 1992). Third, they can show a lack of nutrient limitation in situations where factors other than nutrients (e.g., light) control phytoplankton growth (Hecky and Guildford 1984; Guildford et al. 1987; Agusti et al. 1990). Fourth, they can explain competitive interactions of phytoplankton (Van Donk and Kilham 1990; Sommer 1988, 1989, 1993) because they are an expression of relative growth rates when phytoplankton are nutrient limited (Hecky and Kilham 1988). The nutrient status of phytoplankton is also important functionally because it determines the quality of phytoplankton as food for consumers (Smith 1991; Urabe and Watanabe 1992; Sterner et al. 1993), influences the accumulation of organochlorines in the food web (Swackhamer and Skoglund 1993; Taylor et al. 1991), and determines the responses of phytoplankton to toxic metals

[1]This is one in a series of papers describing work of the Freshwater Institute Science Laboratory on a lake-size series in Northwest Ontario (NOLSS) and done in honor of the 25th anniversary of the Experimental Lakes Area.

TABLE 1. Morphometric parameters for the studied lakes. A_0 = lake surface area (net water area, not including the area of islands); A_d = area of the terrestial catchment (not including the lake area); $(A_d + A_0)/V$ = the ratio of total catchment area to lake volume; τ_w = nominal water renewal time; calculated from lake volume, total catchment area, and maps of mean annual runoff; Z_m, maximum depth; $\bar{z}$ = mean depth; SLD = shoreline development (including islands in shoreline length; not calculated for Lakes Nipigon and Superior because of a disparity in map scales); A_e/V_e = ratio of epilimnion sediment area to epilimnion volume in midsummer. The volume of Lake Nipigon was estimated by assuming that its area versus depth curve is the same as Lake Superior's.

	A_0 (ha)	A_d (ha)	$(A_d + A_0)/V$	τ_w (yr)	Z_m (m)	$\bar{z}$ (m)	SLD	A_e/V_e (m^{-1})
Lake 373	29	54	0.278	13.5	21	10.3	1.54	0.074
Green	89	234	0.474	8.6	19	7.7	2.02	0.081
Orange	167	1 100	0.529	7.8	29	14.4	2.31	0.055
Linge	706	2 980	0.624	6.7	23	8.4	2.84	0.104
Musclow	2 220	32 850	0.821	5.0	46	19.2	3.64	0.032
Sydney	5 750	46 400	0.454	9.1	73	20.0	7.40	0.053
Trout	34 700	71 800	0.226	17.5	49	13.6	10.48	0.059
Nipigon	484 800	2 450 000	0.103	25.6	143	58.5		0.007
Superior	8 223 600	21 000 000	0.024	180.4	403	148.7		0.003

(Creed et al. 1990; Twiss and Nalewajko 1992). Therefore, it is important to understand the processes influencing nutrient status.

A primary objective for studying phytoplankton nutrient status along a lake size gradient was to determine whether it is appropriate to apply information from whole ecosystem experimental studies on small lakes such as those in the Experimental Lakes Area (ELA) (Johnson and Vallentyne 1971; Schindler et al. 1990) and from long-term ecological research (LTER) sites (Magnuson et al. 1991) to larger lakes of social and economic interest (e.g., Laurentian Great Lakes). Phytoplankton of small, oligotrophic lakes on the Canadian Shield is extremely nutrient deficient (Healey and Hendzel 1980), whereas the role of nutrients in the Great Lakes is more equivocal (Nalewajko et al. 1981; Harris 1986; Fee et al. 1992). These differences may be a direct function of the size of the system causing differences in physical and chemical conditions. Only by comparing lakes of similar nutrient regimes can the physical effects of lake size be determined.

Conceptual models (Margalef 1978; Legendre and Demers 1984; Harris 1986) state that phytoplankton processes should be increasingly linked to physical processes in lakes of increasing size because large lakes have more vigorous horizontal and vertical water motions and thus produce higher levels of turbulent kinetic energy. An increasing number of physical processes come into play at increasing length scales (Boyce 1974). We examine this observation by determining and comparing phytoplankton nutrient status along a gradient of increasing lake size (29 – 8.223 × 10^6 ha).

To compare lake systems of different sizes, temporal variance must be determined and accounted for by comparative statistical analysis. Measurements over a range of time intervals can identify relationships or differences among lakes. Temporal events range from short-lived phenomena, such as an upwelling event (scale of minutes to days), to longer term events, such as annual hydraulic and nutrient loading. Low-frequency events (e.g., El Niño) can only be shown to influence biological processes if the study period is long enough to capture these phenomena. The comparison of factors controlling biological processes on different time scales may lead to important conclusions for lake management. The time scale of sampling used in this study, weeks to 5 yr, neither covered very short time scales, which can be important to phytoplankton, nor long-term events such as decadal climatic variability, but it allowed examination of variability within and between years. The study included some of the warmest years on record as well as average conditions.

During the study, six lakes were sampled 10 times during each open-water season for 6 yr and two large lakes were sampled for 2 yr, producing a total of 400 samples. The lakes were similar with respect to climate, stratification, water residence times (>5 yr), and geology (Canadian Shield) but spanned a considerable range of lake surface areas. The research attempted to capture the natural variability of the study lakes, and the data may provide a benchmark for healthy ecosystems against which suspected perturbations of nutrient cycling in impacted systems can be evaluated.

Methods

Study Area and Design

The nine lakes of the Northwest Ontario Lake Size Series (NOLSS) study are located on the Canadian Shield within the north temperate climatic region (Fee and Hecky 1992). Only Lakes Nipigon and Superior have permanent human settlements in their basins, but these are few relative to the large size of the lakes. The surface areas of the nine lakes form an approximately logarithmic series from ELA Lake 373 (29 ha) to Lake Superior (8.223 × 10^6 ha) (Table 1).

Field Sampling

The lakes were sampled from ice-out (early May in the small ones) to mid-October at intervals of ≤3 wk from 1986 to 1991. Sampling was more frequent immediately after ice-out (weekly) and less frequent after stratification in early June (every 3 wk). Samples were usually taken at maximum depth or, for Lakes Nipigon and Superior, at an offshore location chosen on the basis of previous surveys (Fee and Hecky 1992). Integrated whole water samples were taken over 0–3 m, and stored at in situ temperatures in the dark for 2–6 h before analyses. Concentrated net plankton samples were collected by taking surface tows with a 10-μm mesh net.

TABLE 2. Values indicative of presence or absence or degree of nutrient deficiency for nutrient status indicators used in this study. C = carbon; N = nitrogen; P = phosphorus; chl = chlorophyll *a*; APA = alkaline phosphatase activity.

Indicator	Nutrient	No deficiency	Moderate deficiency	Extreme deficiency	Deficient
C/N[a]	N	<8.3	8.3–14.6	>14.6	
C/P[a]	P	<129	129–258	>258	
C/chl[b]	N or P	<4.2	4.2–8.3	>8.3	
(APA·chl^{-1})[c]	P	<0.003	0.003–0.005	>0.005	
N/P[a]	P	<22			>22
N debt[d]	N	<0.15			>0.15
P debt[e]	P	<0.075			>0.075

[a]Atomic ratio.
[b]μmol C·μg chl^{-1}.
[c]Particulate APA, μmol P·μg chl^{-1}·h^{-1}.
[d]μmol N·μg chl^{-1}.
[e]μmol P·μg chl^{-1}.

In situ measurements included light and temperature profiles. Light attenuation was measured with a Li-Cor LI-185 underwater quantum sensor (flat plate, cosine-corrected collector). Daily mean photosynthetically available radiation (PAR) in the mixed layer ($\bar{I}$) was calculated as

$$\bar{I} = \bar{I}_s \frac{\int_0^{Z_{mix}} A(z)I(z)dz}{\int_0^{Z_{mix}} A(z)dz}$$

where $\bar{I}_s$ is the mean solar flux at the surface of the lake during the day (24-h average), Z_{mix} is the mixing depth, $I(z)$ is the fraction of the surface solar radiation that penetrates to depth z, and $A(z)$ is the area of the lake at depth z. $\bar{I}_s$ was calculated with simulated cloud-free solar data (Fee 1990).

Manual resistance thermometers were used to measure temperature as a function of depth in the NOLSS lakes in 1986 and 1987; Lake 373 was measured in all years. A free-falling temperature profiler that measured temperature at depth intervals of ≈0.05 m was used in other lakes and years (R. Brancker Research Ltd., Ottawa, ON). Mixed-layer depths were taken as the maximum rate of change of temperature with depth, and normally exceeded 1.0°C·m^{-1}.

Laboratory Procedures

Water samples were subdivided for chemical analyses, plankton identification and counting, nutrient status measurements, and photosynthetic rate measurements. Unless otherwise specified, chemical analyses were done using the methods of Stainton et al. (1977). Chlorophyll *a* (chl) was determined by filtering 100 mL of water through a GF/C filter. The filter was placed in a glass vial, 10 mL of 95% methanol was added, and the vial was frozen at −10°C and allowed to stand overnight (at least 16 h). The extract was agitated, allowed to settle, and its fluorescence was assayed on a Turner Model 110 fluorometer. The fluorometer was routinely standardized with a chl solution (Sigma Chemicals) the stability of which was verified using an HP scanning spectrophotometer. In 1986, chl extracts were not always mixed prior to reading fluorescence; this introduced a serious and inconsistent bias, so data from 1986 are not reported.

Phytoplankton photosynthesis rates per unit volume at different light intensities were measured using the ^{14}C incubator method (Fee et al. 1989). Photosynthesis parameters (P_m^B and α^B) and in situ integral photosynthesis were estimated using the computer programs of Fee (1990). P_m^B is the light-saturated rate of photosynthesis per unit of chl, and α^B is the slope of the light-limited part of the photosynthesis-light curve normalized to chl (photosynthetic efficiency). P_{opt} (the light-saturated rate of photosynthesis) was normalized to particulate carbon (C) as an independent measure of C turnover and was used as an estimate of relative growth rate.

Phytoplankton nutrient status measurements consisted of four seston composition ratios (C/nitrogen (N), C/phosphorus (P), C/chl, and N/P) and two metabolic indicators (alkaline phosphatase activity (APA) and N debt, both expressed per unit chl). During 1987, P debt and $^{32}PO_4^{3-}$ turnover time were also measured. Particulate C, N, and P samples from both whole water and net samples were filtered through preignited GF/C filters and the filters were kept frozen until analyzed (Stainton et al. 1977). Nutrient composition ratios were calculated on an atom:atom basis for C/N, C/P, and N/P, and an atom:weight basis for C/chl.

Alkaline phosphatase activity, an indicator of P deficiency, was measured fluorometrically (Healey and Hendzel 1979a) using 5-μM *o*-methyl-fluorescein-phosphate as the substrate. Parallel determinations were made of total and soluble activities to distinguish between APA associated with particles and APA in solution; the soluble activity was that passing through 0.2-μm filters. The difference is reported as particulate activity. APA was routinely normalized to chl; however, APA was also normalized to P_{opt} as a biomass-independent nutrient status indicator.

The N-debt assay was used in conjunction with particulate C/N ratios to determine N deficiency. The assay is based on the work of Healey (1977) who demonstrated that several species of algae took up more ammonium (NH_4^+) when N deficient than when N sufficient. For the N debt assay, 100 mL of unfiltered sample was enriched with ammonium chloride to yield a final concentration of ≈5 μM N. Ammonium was measured (Stainton et al. 1977) on triplicate subsamples at the beginning and end of the incubation. Samples were incubated in the dark at room temperature. Nitrogen debt was calculated as the nutrient removed over a 24-h period per unit of chl (Healey 1977). Nitrogen-debt values

TABLE 3. Percentages of the total sums of squares resulting from analysis of variance of physical, chemical, and biological variables for four categories: lake, year, month, and unexplained. APA = alkaline phosphatase activity; chl = chlorophyll *a*; C/P, C/N, N/P = particulate carbon, nitrogen, and phosphorus atomic ratios; N debt = nitrogen debt per unit chl; α^B, slope of the light limited part of the photosynthesis-light curve normalized to chl; P_m^B = light-saturated rate of photosynthesis normalized to chl; $P_{opt} \cdot C^{-1}$ = light-saturated rate of photosynthesis normalized to particulate C; TP = total phosphorus; TN = total nitrogen; SRSi = soluble reactive silicon; DOC = dissolved organic carbon; $\bar{I}$ = mean water column light intensity in the mixed layer; Z_{mix} = mixed depth; Ext = light extinction coefficient; Secchi = Secchi disk depth.

	Lake	Year	Month	Unexplained
Biological				
APA·chl^{-1}	38	15	4	43
C/P	39	4	6	51
C/chl	62	9	0	29
C/N	27	8	5	60
N/P	16	4	1	79
N debt	12	1	5	82
chl	74	7	1	18
α^B	9	25	8	57
P_m^B	5	12	2	81
$P_{opt} \cdot C^{-1}$	51	2	0	47
Chemical				
TP	69	4	1	26
TN	84	1	0	15
SRSi	90	3	0	7
Alkalinity	100	0	0	0
DOC	92	2	1	5
Physical				
$\bar{I}$	43	2	40	15
Temperature	40	8	10	42
Z_{mix}	43	7	9	41
Ext	88	1	1	9
Secchi	77	1	6	17

for Lakes Nipigon and Superior are not reported because of methodological problems with the NH_4^+ analysis. Phosphorus debt was measured in a similar way to N debt except that potassium dihydrogen phosphate was added (final concentration 5 μM). Soluble reactive phosphorus (SRP) was measured on triplicate subsamples passed through GF/C filters (Healey 1975). Phosphorus turnover times were measured using ^{32}P following the method of Lean and Nalewajko (1979). Statistically significant agreement existed among the three P deficiency indicators (APA, P debt, and $^{32}PO_4^{3-}$ turnover times), confirming that all three physiologically based methods agreed on the P nutrient status in these lakes (S.J. Guildford and L.L. Hendzel, unpublished data). In subsequent years, P nutrient status was measured using APA per unit chl. Elemental composition of the seston was measured using both whole water and net samples over the duration of the study. Paired *t*-tests of the ratios indicated that there was no significant difference between the two types of samples (S.J. Guildford and L.L. Hendzel, unpublished data). The limits for the various types and degrees of nutrient deficiency indicated by both the seston composition ratios and metabolic assays are given in Table 2.

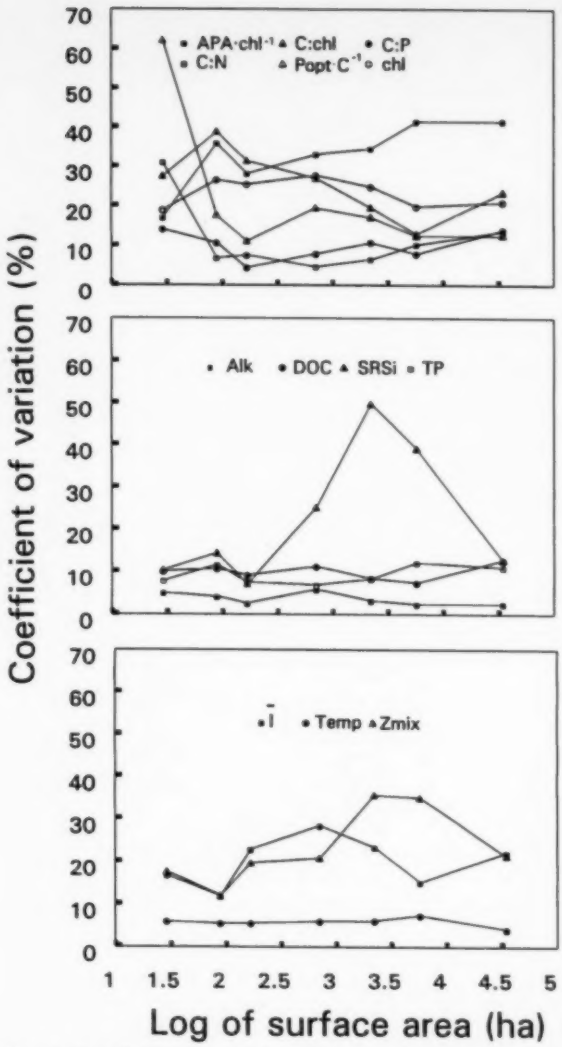


FIG. 1. Coefficient of variation for seasonal means (June 1 – September 30, 1987–91) for biological, chemical, and physical variables plotted as a function of lake size. Lakes Nipigon and Superior are not included. Abbreviations as in Table 3.

Data Analysis

Data were transformed using ln or ln + 1 to achieve more normal distributions and variances independent of their means, and to deal with zero values (N debt data) (Elliott 1983; Hanna and Peters 1991). Bartlett's test (Steel and Torrie 1960) was used to test the hypothesis that variances were homogeneous (HGV) and analysis of variance (ANOVA) was used to test the hypothesis that means were equal. When the assumption of HGV was not met, 0.001 was chosen as the probability below which both hypotheses were rejected. When ANOVA results indicated means were not equal, further comparisons were conducted using Tukey HSD multiple comparison tests (Steel and Torrie 1960). Relative contributions of lakes, years, months, and

TABLE 4. Five year geometric means of physical, chemical, and biological variables (June 1 – September 30, 1987–91). Lake names are abbreviated to their first three letters (see Table 1). Abbreviations as in Table 3; units as in Fig. 2. HGV = Bartlett's test for homogeneity of variance; ANOVA = analysis of variance.

	373	Gre	Ora	Lin	Mus	Syd	Tro	Nip	Sup	HGV	ANOVA
Biological											
APA·chl^{-1}	0.126	0.102	0.083	0.050	0.030	0.035	0.059	0.026	0.067	0.006	0.000
C/P	434	439	386	340	269	268	302	234	309	0.273	0.000
C/chl	40	29	19	17	13	15	20	12	19	0.000	0.000
C/N	13.8	12.4	11.4	11.2	10.2	11	11.2	8.9	10.4	0.000	0.000
N/P	31.5	35.5	33.9	30.3	26.4	24.5	27	26.3	29.8	0.003	0.000
N debt	0.33	0.14	0.13	0.08	0.10	0.05	0.12	NA	NA	0.00	0.007
chl	0.82	1.83	2.73	3.51	4.17	2.79	1.76	2.38	0.89	0.106	0.000
α^B	3.06	3.61	3.50	4.13	4.42	3.93	3.91	4.04	3.22	0.009	0.005
P_m^B	2.55	2.45	2.18	2.52	2.51	2.37	2.6	2.74	1.92	0.082	0.121
P_{opt}·C^{-1}	0.07	0.08	0.11	0.15	0.19	0.16	0.13	0.23	0.10	0.000	0.000
Chemical											
TP	0.17	0.24	0.27	0.33	0.40	0.32	0.24	0.25	0.15	0.000	0.000
TN	15.2	22.5	23.4	25.8	28.2	22.2	15.5	17.5	28.5	0.000	0.000
SRSi	23.9	8.1	26.6	14.8	5.2	2.5	33.3	49.0	39.9	0.000	0.000
Alkalinity	176	187	374	220	352	300	562	1395	796	0.007	0.000
DOC	308	507	666	602	719	523	322	407	146	0.000	0.000
Physical											
$\bar{I}$	16.06	10.93	7.16	7.4	5.05	6.99	7.77	6.12	8.63	0.875	0.000
Temperature	19.70	18.89	18.88	18.39	17.88	17.47	16.01	13.81	8.83	0.000	0.000
Zmix	5.26	5.71	5.78	7.11	7.72	7.89	12.44	11.57	24.37	0.000	0.000
Ext	0.284	0.456	0.613	0.615	0.614	0.478	0.345	0.439	0.174	0.002	0.000
Secchi	7.0	4.4	3.7	3.4	3.6	4.8	5.7	5.2	12.0	0.025	0.000

unexplained variance to the total sums of squares for each variable were calculated from ANOVAs.

Principal components analysis (PCA) was done on ln-transformed, standardized data. The data were standardized because the variables encompassed a wide range of scales. Data were standardized for each variable by subtracting the mean and dividing by the standard deviation (SD). This resulted in all variables having a mean of 0 and an SD of 1. Principal components analysis was done on a correlation matrix of the annual means (June 1 – September 30, unless otherwise stated) for each lake. We hypothesized that nutrient status (and other biological variables) are a multivariate function of the physical and chemical variables in a lake. If lakes are ordinated along multivariate axes for physical and chemical variables, then it should be possible to correlate nutrient status variables (and other biological variables) against these axes. The variables used in the PCA were total phosphorus (TP), total nitrogen (TN), soluble reactive silicon (SRSi), dissolved organic carbon (DOC), alkalinity (Alk), temperature (Temp), light extinction (Ext), and Z_{mix}. Various rotations were tried and the Quartimax rotation was selected because it gave the best separation of variables. Statistical analyses were done using SYSTAT (Wilkinson 1990).

Results

Natural Variability

For all but two of the variables (P_m^B and α^B), the majority of the explained variation was caused by lake-to-lake differences (Table 3). Biological variables (except chl) had higher proportions of unexplained variation than the chemical and physical variables. No consistent increase or decrease in variation was observed among years for seasonal means of biological, chemical, and physical variables with changing lake size (Fig. 1).

Plots of the geometric means (±95% confidence intervals (CI)) for the 5 yr of data for each variable and lake against $\log_{10}$ lake size (Fig. 2A and 2B) emphasized trends apparent in Table 3. Total N, TP, SRSi, DOC, alkalinity, Ext, Secchi depth, and chl (Fig. 2A and 2B) had strong lake-to-lake variation and narrow CIs. The remaining variables had wider CIs but, except for P_m^B and α^B, more lake-to-lake than within-lake variation was still evident. The lakes differed from each other for most variables (ANOVA, $P < 0.001$; Table 4). However, Tukey HSD multiple comparisons for individual variables (not given) indicated no consistent pattern in the lake-to-lake differences.

Phytoplankton Nutrient Status

Nutrient status indicators for P (APA·chl^{-1}, C/P, and N/P) indicated that all nine lakes were strongly P deficient (Fig. 2A). Carbon/chl, often used as a general nutrient status indicator (Healey and Hendzel 1980), had a pattern similar to the P nutrient status indicators (Fig. 2A). Nitrogen debt and C/N (Fig. 2A) indicated that the smallest lake, 373, also bordered on extreme N deficiency. The remaining lakes were moderately N deficient, according to the C/N ratio, but were not usually N deficient, using N-debt data, although the spread in the CIs showed that N debt occurred occasionally in all of the lakes. An almost linear relationship appeared to exist between nutrient deficiency indicators and lake size for the five smallest lakes in the size series (373, Green, Orange, Linge, Musclow) but the relationship became nonlinear as the larger lakes were included (Fig. 2A).

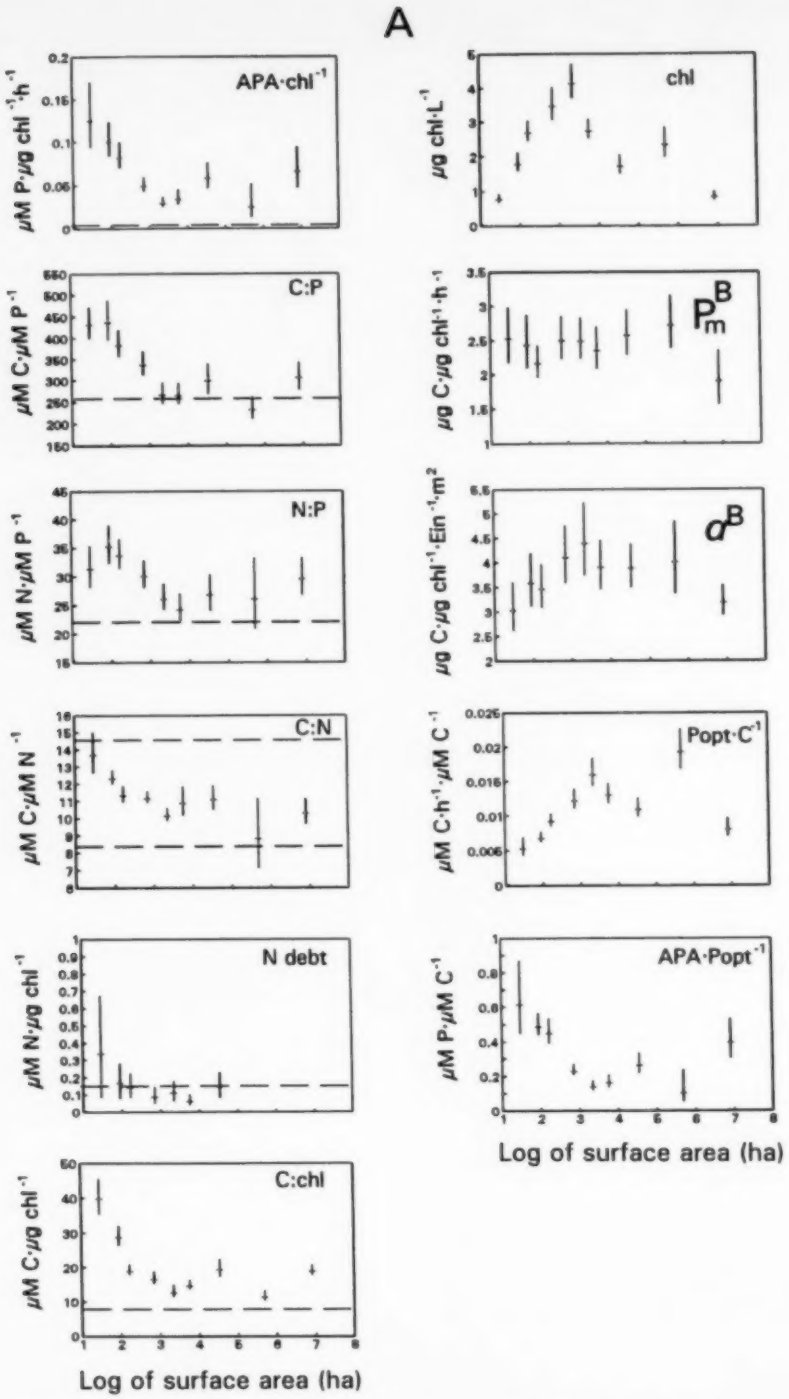


FIG. 2. (A) Seasonal means and 95% confidence intervals (CI; vertical bars) for biological variables (June 1 – September 30, 1987–91) plotted as a function of lake size. Values above broken lines indicate nutrient deficiency (see Table 2). (B) Seasonal means and 95% CIs for chemical and physical variables (June 1 – September 30, 1987–91) plotted as a function of lake size. Abbreviations as in Table 3. (*Fig. 2 concluded next page*)

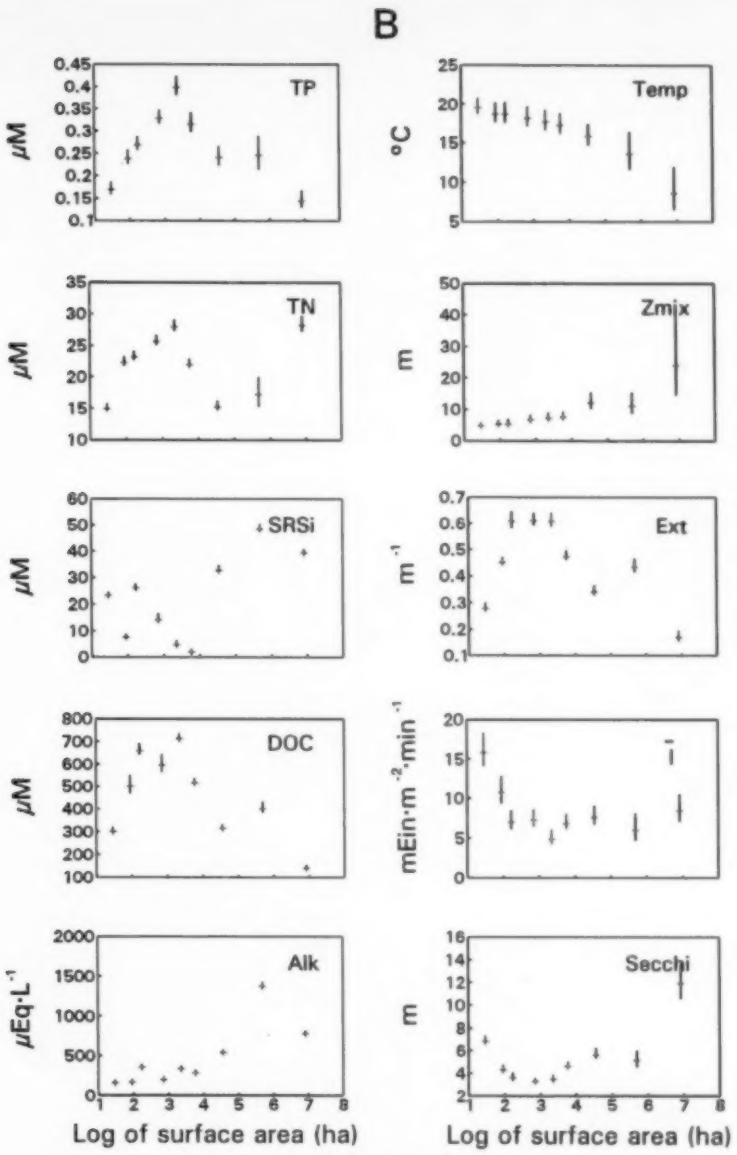


FIG. 2. (*Concluded*)

Chlorophyll *a* and Photosynthesis

Mean chl concentrations were all in the oligotrophic range (<7.0 mg·L^{-1}) (Marshall and Peters 1989). Chlorophyll *a* showed a mirror image to the pattern of the P deficiency indicators (including those not normalized to chl): an almost linear increase with increasing lake size for the five smallest lakes but then a decrease in the larger lakes (Fig. 2A). Only the photosynthetic parameters, P_m^B and α^B, did not vary significantly among lakes. Tests of the hypothesis that no lake-to-lake differences exist in means for each variable indicated that only P_m^B, α^B, and N debt had probabilities >0.005 that their means were equal (Table 4). P_{opt} normalized to particulate C and APA normalized to P_{opt} (Fig. 2A) exhibited the same distribution over lake size as the nutrient status indicators, i.e., a linear change with size in small systems, and a plateau or reversal at larger sizes.

Chemical Variables

Total P (Fig. 2B), like chl and the P nutrient status indicators (Fig. 2A), increased with increasing lake size for the five smallest lakes, but decreased in the larger lakes; Lake Superior had the same mean TP as Lake 373. The mean TN trend was similar to that of TP except that Lake Superior had the highest TN. Green, Musclow, and Sydney lakes had low Si. The DOC trend was similar to TP, whereas alkalinity increased with lake size (Fig. 2B).

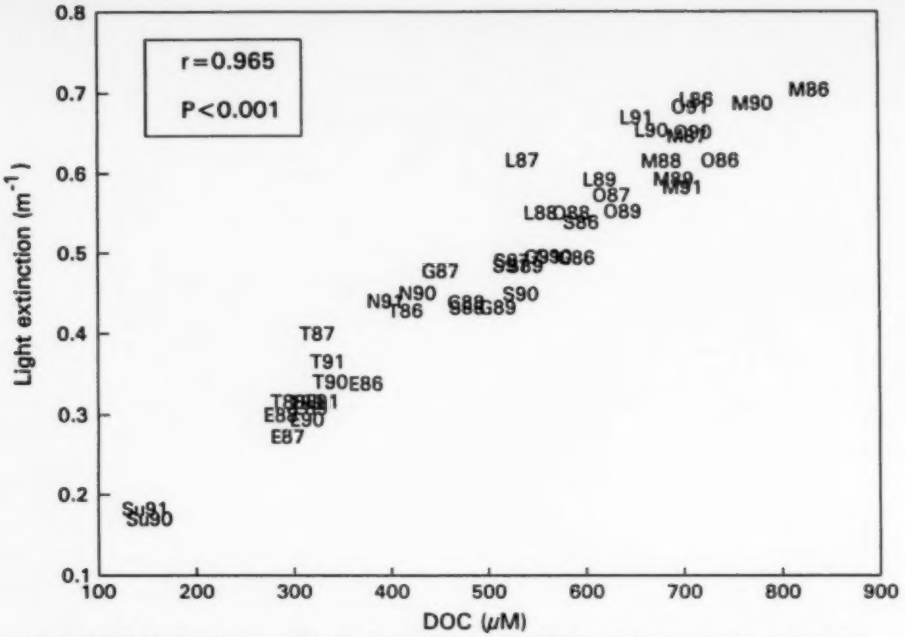


FIG. 3. Relationship between dissolved organic carbon (DOC) and light extinction in the nine study lakes. Values are seasonal means (June 1 – September 30, 1986–91). The first character of each symbol is the first letter of the lake name, except for Lake Superior (Su). The letters are followed by the years (86 = 6, 87 = 7, etc.).

TABLE 5. Principal components (PC) analysis of a correlation matrix of the annual means of eight selected chemical and physical variables from the nine study lakes. Other abbreviations as in Table 3.

	PC1	PC2	PC3	PC4
Rotated loadings				
Ext	0.955	−0.225	−0.061	0.098
TP	0.918	0.042	0.277	0.050
DOC	0.913	−0.345	0.021	0.082
Alkalinity	0.037	0.918	−0.247	−0.174
Z_{mix}	−0.289	0.910	0.075	0.061
Temperature	0.414	−0.836	0.012	−0.290
SRSi	−0.408	0.240	−0.857	−0.142
TN	0.494	0.105	0.159	0.841
Variance explained by rotated loadings	3.254	2.611	0.908	0.864
Percentage of total variance explained	40.674	32.631	11.345	10.797

Physical Variables

Temperature and Z_{mix} were clearly size related (Fig. 2B). Light extinction remained relatively constant within each lake (Fig. 2B) and was highly correlated with DOC (Fig. 3), indicating that DOC is an effective attenuator of PAR in all the lakes. $\bar{I}$, which is calculated from Ext and Z_{mix}, was not related to lake size; the smallest (373, Green) and largest (Superior) lakes had the three highest mean water column light intensities (Fig. 2B). The lowest mean $\bar{I}$ occurred in Musclow Lake, which also had the lowest extinction value and highest DOC.

Principal Components Analysis of the Physical and Chemical Variables

The first principal component (PC1), which explained 41% of the total variance, primarily contained Ext, TP, and DOC (Fig. 4; Table 5). PC2, which primarily contained alkalinity, Z_{mix}, and temperature explained 33% of the total variance. PC3 (SRSi) and PC4 (TN) each explained 11% of the variance. The PCA revealed that different years grouped tightly together for individual lakes (Fig. 4), indicating that variation due to year-to-year differences was much less important than the lake-to-lake differences for the variables measured (Table 3).

The highest loadings on PC1 (Ext, TP, DOC) were essentially chemical variables; although Ext is a physical measurement, Ext is highly correlated to the chemical variable DOC (Fig. 3). Two of the three highest loadings on PC2 (Z_{mix}, tempearture) were physical variables. In these lakes, temperature and Z_{mix} were correlated with lake size (r = 0.941, $P < 0.001$, $n = 9$ and $r = 0.809$, $P < 0.01$, $n = 9$, respectively), so a good correlation existed between log lake area and PC2 ($r = 0.966$, $P < 0.001$). This correlation was strengthened by the fact that alkalinity was higher in the large lakes than in the small ones. Large lakes on the Canadian Shield may be enriched by carbonate minerals; the larger the watershed, the higher the probability of encountering glacial deposits that yield carbonate alkalinity (Fee and Hecky 1992).

PC3 was dominated by SRSi (Fig. 4); Green, Musclow, and Sydney lakes had distinctly lower SRSi concentrations than the other lakes (Table 4). PC4 was dominated by TN; Trout Lake, Lake Nipigon, and Lake 373 had the lowest mean TN concentrations, whereas Lake Superior had the highest.

TABLE 6. Correlation coefficients between the annual means of the biological variables and the scores for each lake year from the principal components (PC) analysis of the physical and chemical variables described in Fig. 4 and Table 5. Columns 1 and 2 are the simple correlation coefficients between the biological variables and the chemical (PC1) and physical (PC2) axes. Column 3 is the multiple linear correlation coefficient between the biological variables and PC1 + PC2. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Abbreviations as in Table 3.

Biological variables	PC1 Chemical	PC2 Physical	PC1 + PC2
APA·chl^{-1}	−0.462**	−0.471**	0.705***
C/P	−0.386*	−0.699***	−0.799***
C/chl	−0.623***	−0.606***	0.869***
C/N	−0.426**	−0.633***	0.763***
N/P	−0.202	−0.485**	0.525**
N debt	−0.601***	0.113	0.602***
chl	0.912***	0.149	0.924***
αB	0.27	0.124	0.297
P^B_m	0.002	−0.123	0.123
P_{opt}·chl^{-1}	0.597***	0.513**	0.787***
APA·$P_{opt}{}^{-1}$	0.512**	0.482**	0.752***
$\bar{I}$	−0.739***	−0.571***	0.934***

Relationship of Biological to Physical and Chemical Variables

If the biological variables are a function of the physical and chemical features of the lakes, then a relationship should be evident between the biological variables and the PCA axes (especially PC1 and PC2, which accounted for most (74%) of the physical and chemical variance among lakes). Chlorophyll *a* was highly correlated with PC1, the largely chemical axis ($r = 0.912$). Addition of PC2, the physical axis, yielded a slightly improved correlation ($r = 0.924$). Nutrient status indicators, APA·chl^{-1}, C/P, C/N, and C/chl were more highly correlated with the multiple linear combination of PC1 + PC2 than with either axis alone (Table 6), as were P_{opt}·C^{-1} and APA·$P_{opt}{}^{-1}$. P^B_m and α^B were not strongly correlated to either or both axes, which is not surprising because they did not exhibit significant lake-to-lake differences.

Discussion

Natural Variability

Most of the variability in the data within the open-water season over the 5 yr studied was caused by lake-to-lake differences rather than yearly or monthly differences (Table 3), despite the fact that the study area experienced hot, dry years (1987, 1988) and extremely wet years (1990, 1991; Fig. 5). Hanna and Peters (1991) reported similar results in their study of 16 lake basins located in a uniform climatic and geologic region. Total P and chl variance was much greater among lakes than among times (years, sampling dates) or sampling protocols. The low seasonal variability relative to interlake variability in our study can be partly attributed to the oligotrophic nature of our study lakes (cf. eutrophic lakes; Marshall and Peters 1989).

Site replication can be a minor source of variance (Hanna and Peters 1991) but this was not addressed in the study. Patalas and Salki (1993) examined zooplankton patchiness in the NOLSS lakes and found much less variability in replicated samples from offshore than nearshore sites. Low year-to-year variability and significant interlake differences (Table 4) indicate that biological variables are annually typical in the lakes, and that few samples are necessary to characterize nutrient status for lakes of this region.

The NOLSS study originally hypothesized that natural interannual variability is an inverse function of size (Fee

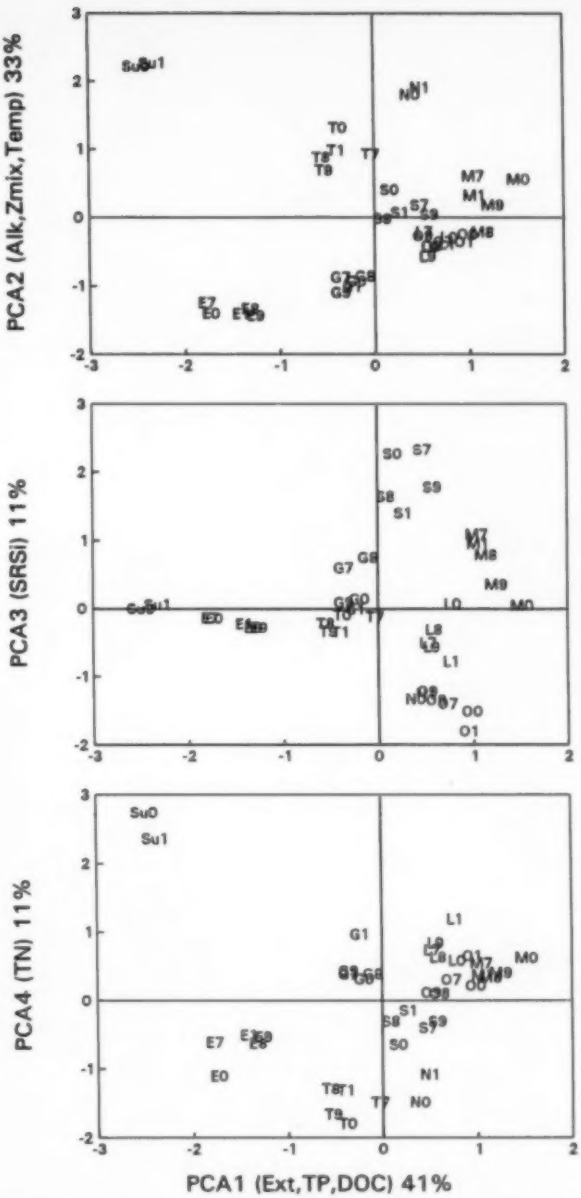


FIG. 4. Lake–year loadings for the first four axes of the principal components analysis. The first character of each symbol is the first letter of the lake name, except for Superior (Su). The letters are followed by the years (87 = 7, 88 = 8, etc.). Abbreviations as in Table 3.

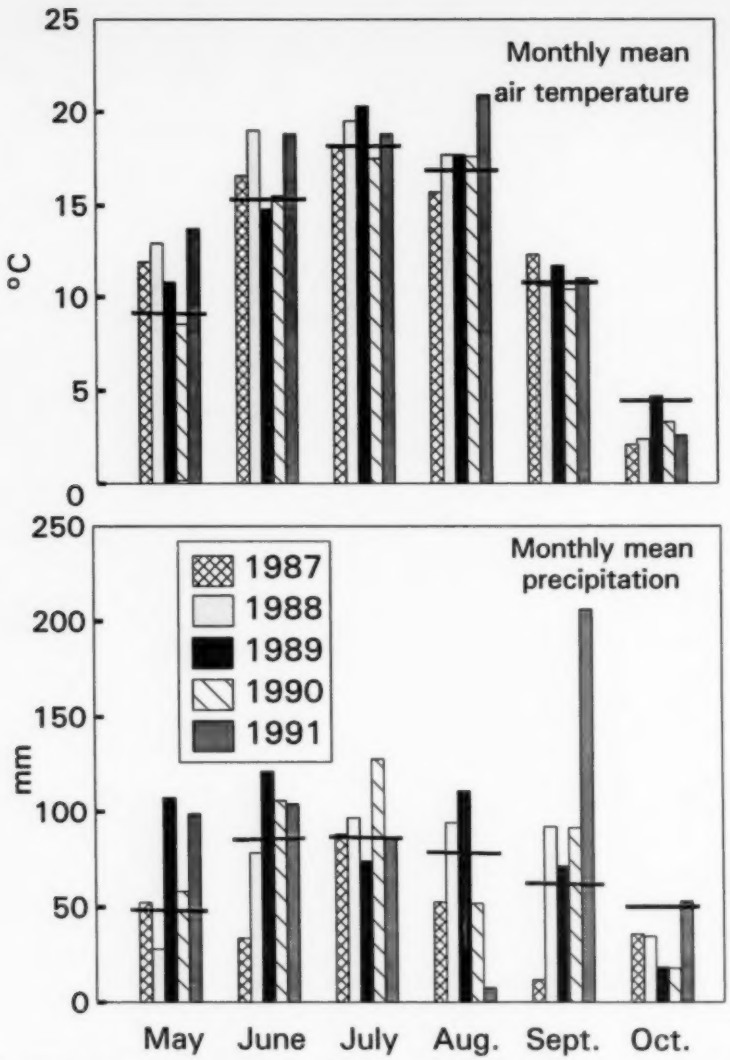


FIG. 5. Monthly mean air temperature (top panel) and monthly mean precipitation (bottom panel) at Red Lake, Ontario, for 1987–91. The solid horizontal line for each month represents the long-term (1950–81) monthly mean.

and Hecky 1992), based on the assumption that large bodies of water would be more buffered than small ones against extreme events. However, the coefficient of variation for nutrient status, and chemical and physical variables showed no tendency to decrease with increasing lake size (Fig. 1), although data from lakes Nipigon and Superior, the two largest lakes, were incomplete and were not included. Fee et al. (1992) also found no relationship between interannual variability of P_m^B and α^B and lake size.

The biological variables, with the exception of chl, had a high proportion of unexplained variation (Table 3), probably because of analytical error and inappropriate sampling scales. Analytical error is high because the biological variables are mostly ratios (to correct for biomass), and errors inherent in the dividend and divisor are included in the quotient. The spatial and temporal scales of triweekly sampling at one station are not directly relevant to the scale of phytoplankton cellular processes (Reynolds 1984; Harris 1986) because significant changes can occur on a daily basis over short distances. In spite of the large unexplained variation, all but three of the biological variables were significantly different among lakes (Table 4).

Phytoplankton Nutrient Status

All nine lakes were extremely P deficient, according to the criteria suggested by Healey (1975); inferred growth rates were low (<20% of maximum). APA·chl^{-1} values were >0.005 μM P·μg chl^{-1}·h^{-1}, C/P seston ratios were >258 (except Lake Nipigon: 234), and all N/P seston ratios were >22. The assignment of extreme P deficient status was based on 5 yr mean values for June 1 – September 30. Within seasons, P deficiency ranged from none to extreme (Fee

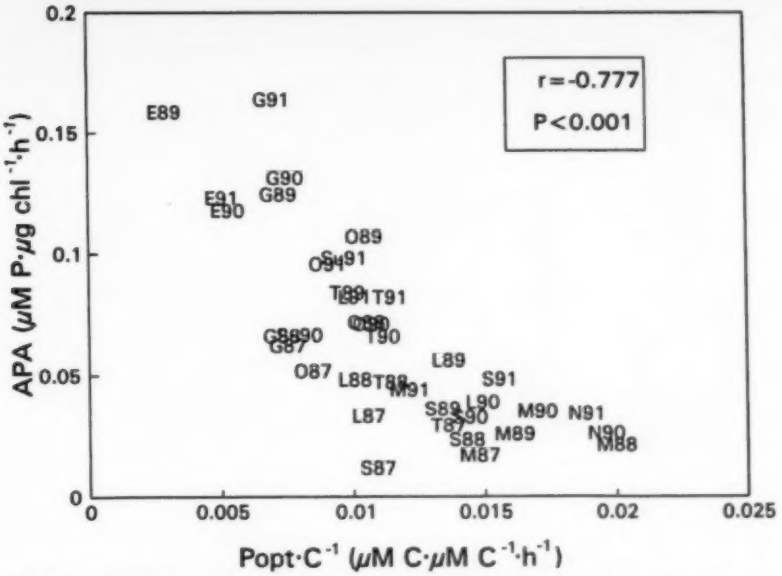


FIG. 6. Relationship between the maximum rate of light-saturated photosynthesis (P_{opt}) normalized to particulate carbon (C) and alkaline phosphatase activity (APA) normalized to chlorophyll *a* (chl) in the nine study lakes. Values are seasonal means (June 1 – September 30, 1987–91). The first character of each symbol is the first letter of the lake name, except for Lake Superior (Su). The letters are followed by the years (87 = 7, 88 = 8, etc.).

et al. 1989). In spite of the extreme P deficiency in all lakes, consistent differences were evident in the degree of P deficiency among lakes. The three smallest lakes were always more strongly P deficient by all indicators than the remaining larger lakes (Fig. 2A).

Similar degrees of P nutrient status were observed from seasonal studies done on epilimnetic samples from other stratified Canadian Shield lakes. Healey and Hendzel (1980) reported extreme P deficiency in seven lakes in the ELA using similar indicators (APA·chl^{-1}, C/P, N/P seston ratios, P debt). Lean et al. (1987) and Pick (1987), using phosphate turnover times, the phosphate deficiency index (PDI), and total APA, classified offshore station 403 of Lake Ontario as strongly P deficient throughout the stratified period; they also showed that the smaller (500 ha) Sharpes Bay on Jacks Lake, Ontario, was much more strongly P deficient than Lake Ontario.

Carbon/nitrogen atomic ratios indicated that all the lakes were moderately N deficient. Mean N-debt values indicated that only Lake 373 was N deficient. The composition ratios gave a different impression than the metabolic uptake measurement of N status. Composition ratios indicated that N as well as P was in short supply in the lakes. However, C/N composition ratios indicate only moderate N deficiency and N debt rarely indicates N deficiency. The uptake processes for these nutrients require energy, which may have been directed toward the more deficient nutrient, P, in these lakes. Cooccurrence of P and N deficiency as observed in Lake 373 has been reported from other ELA lakes (Fee 1979) and can be expected in natural communities with a mixture of phytoplankton species. Suttle et al. (1991) used size fractionation techniques and uptake rates of both P and N to conclude that simultaneous N and P deficiency in oligotrophic Sproat Lake, British Columbia, was caused by the presence of two species: N-deficient *Synechococcus* and a P-deficient diatom. The presence of N_2-fixing cyanoprokaryotes[2] and detection of N_2-fixation are other indicators of N deficiency. Surprisingly, the lakes that had the highest C/N ratios (373 and Green, which were also the most P-deficient lakes) had the lowest biomass of N_2-fixing cyanoprokaryotes (H.J. Kling, unpublished data). Samples were routinely analyzed for N_2-fixation in these lakes (acetylene reduction method) but detectable fixation in unconcentrated samples was rarely observed. However, maximal rates of N_2-fixation were observed in samples concentrated by a 10-μm net in Linge and Musclow lakes (Fee et al. 1994).

Although we did not conduct nutrient status measurements for Si, we noted that Si concentrations were routinely <5 μmol in Green Lake and <2 μmol in Sydney and Musclow lakes. In the larger lakes (Sydney and Musclow), where P was not as strongly limiting as in the smaller lakes, Si was probably an intermittent limiting factor for diatoms (Levasseur et al. 1990).

Relative Growth Rates

Droop (1968, 1970) described the growth rate of nutrient-limited phytoplankton as a function of the internal cell quota of the limiting nutrient using the following general equation

$$\mu = \bar{\mu}[1 - (kq/Q)]$$

where μ is the specific growth rate; $\bar{\mu}$ is the specific growth rate at infinite internal substrate concentration; Q is the cell quota of the limiting nutrient; and kq is the subsistence quota, Q at $\mu = 0$. This equation expresses the basic theory

[2]We use the term "cyanoprokaryote" as proposed by Kling et al. (1994) in lieu of blue-greens, blue-green algae, or cyanobacteria.

TABLE 7. Simple and stepwise multiple linear regression equations for the dependence of chorophyll a (chl, $\mu g \cdot L^{-1}$) on total phosphorus (TP, μM), and mean water column light intensity in the mixed layer ($\bar{I}$, $mE \cdot m^{-2} \cdot min^{-1}$). Data were seasonal means for the period June 1 – September 30, 1987–91, for all lakes except Nipigon and Superior (seasonal means, 1990–91).

Equation	r^2	n	P
$\log(chl) = -1.299 + 1.787\log(TP)$	0.876	39	0.001
$\log(chl) = -0.626 + 1.437\log(TP) - 0.389 \log(\bar{I})$	0.906	39	0.001

underlying several nutrient status measurements based on seston composition ratios such as C/P, C/N, and N/P. Application of the theory presumes that the seston ratios are representative of living material. In Canadian Shield lakes with residence times >6 mo, these ratios are representative of living material (Healey and Hendzel 1980; Hecky et al. 1993). Elemental ratios in seston collected on a GF/C filter were compared with those collected with a 10-μm net. The net concentrates larger living cells, which should have a different ratio than whole-water seston if detritus has different ratios than living material. The comparison revealed no significant differences between the two types of samples (paired *t*-test; S.J. Guildford and L.L. Hendzel, unpublished data), which agrees with the results of Healey and Hendzel (1980).

As with the composition ratios, the metabolic measurements (APA, P debt, N debt) were calibrated with respect to nutrient-limited cultures and their cell nutrient quotas growing at different growth rates set by the limiting nutrient (Healey 1975; Healey and Hendzel 1979b, 1980). These uptake and activity indicators were directly proportional to the degree of nutrient deficiency and inversely proportional to growth rate. Thus, Lakes 373, Green, and Orange should have low relative growth rates, whereas Musclow Lake and Lake Nipigon should have high relative growth rates, based on the metabolic nutrient status indicators. The metabolic measurements, like the composition ratios of natural samples, represent more than pure phytoplankton. Our APA measurements included phosphatase activity produced by bacteria-sized particles >0.2 μm. Bacterial biomass, especially in the late fall, could be double the phytoplankton biomass (H.J. Kling, unpublished data). Because peaks in bacterial biomass appeared in both large and small lakes, and occurred when APA was generally low, the trends observed in APA were probably not caused by bacterial activity.

The Droop equation predicts that growth rate varies inversely with nutrient status. Relative rates of growth can be estimated from photosynthetic uptake rates (P_{opt}) normalized to particulate C. The $P_{opt} \cdot C^{-1}$ seasonal means had a pattern that was the mirror image of the nutrient status measurements (Fig. 2A). Measurements of $APA \cdot chl^{-1}$ and $P_{opt} \cdot C^{-1}$ were negatively correlated ($r = -0.777$, $n = 37$, $P < 0.001$; Fig. 6). The ratios C/P, N/P, C/chl, and C/N were also significantly negatively correlated to $P_{opt} \cdot C^{-1}$ ($r = -0.544$ to -0.818, $P < 0.001$). The agreement of the two independent estimators, $APA \cdot chl^{-1}$ and $P_{opt} \cdot C^{-1}$, allowed inferences to be made about relative growth rates in the study lakes. The smallest lakes clearly had the lowest relative growth rates, whereas growth rates in the larger lakes were higher although not strictly defined by size.

It is recognized that correlated ratios each containing C cannot be considered truly independent of each other and that measurements normalized to biomass contain nonliving and living particles as discussed above. To neutralize the biomass estimate, we compared the variable $APA \cdot P_{opt}^{-1}$ among the study lakes. $APA \cdot P_{opt}^{-1}$ is not an established nutrient status indicator, but it is useful because it is independent of either chl or suspended C. It is similar in this respect to the PDI of Lean et al. (1987). $APA \cdot P_{opt}^{-1}$, had the same pattern as $APA \cdot chl^{-1}$ and other biomass-based nutrient status indicators and was the mirror image of $P_{opt} \cdot C^{-1}$ (Fig. 2A). Therefore, the conclusion that nutrient deficiency is lower and relative growth rates higher in large lakes than in small lakes is independent of the normalization of many of these indicators on biomass.

Chlorophyll – Total Phosphorus

Correlation coefficients between the biological variables and PC1 (the chemical axis) and PC2 (the physical axis) demonstrated that chl was readily predicted by the chemical variables. In contrast, the nutrient status and growth rate variables were best predicted by a combination of physical and chemical variables (Table 6).

In P-limited lakes, a statistically significant correlation usually exists between epilimnetic TP and epilimnetic chl (Sakomoto 1966; Dillon and Rigler 1974; Riley and Prepas 1985; Molot and Dillon 1991). Total P concentration can be predicted from annual TP load and flushing characteristics for the lake and drainage area (Dillon and Rigler 1975; Canfield and Bachmann 1981). These TP–chl and TP-flushing relationships have been used as the basis for managing lakes (Dillon and Rigler 1975; Canfield and Bachmann 1981).

A highly significant correlation existed between TP and chl in the nine lakes of this study (Table 7). The C/N and N debt data indicated that N deficiency occasionally cooccurred with P limitation in the lakes and $\bar{I}$ values were sometimes below those reported to limit photosynthesis (Fee et al. 1992), so a multiple stepwise linear regression was done using TN, $\bar{I}$, and TP. Prediction of chl in these lakes was improved statistically by including $\bar{I}$ with TP (Table 7) but the increased amount of variance explained by including $\bar{I}$ was minor.

Physical and Chemical Control of Nutrient Status

The study lakes are all P deficient so it might be expected that the chemical axis can predict both chl concentrations and nutrient status indicators equally well. The fact that significant correlations also required inclusion of physical variables suggested that the nutrient status indicators and growth rates were influenced by both chemical and physical variables. If nutrient status was a simple linear function of TP, then Lake Superior would be as severely P deficient as Lake 373 and Trout Lake would be as severely P deficient as Green Lake because the two sets of lakes have similar

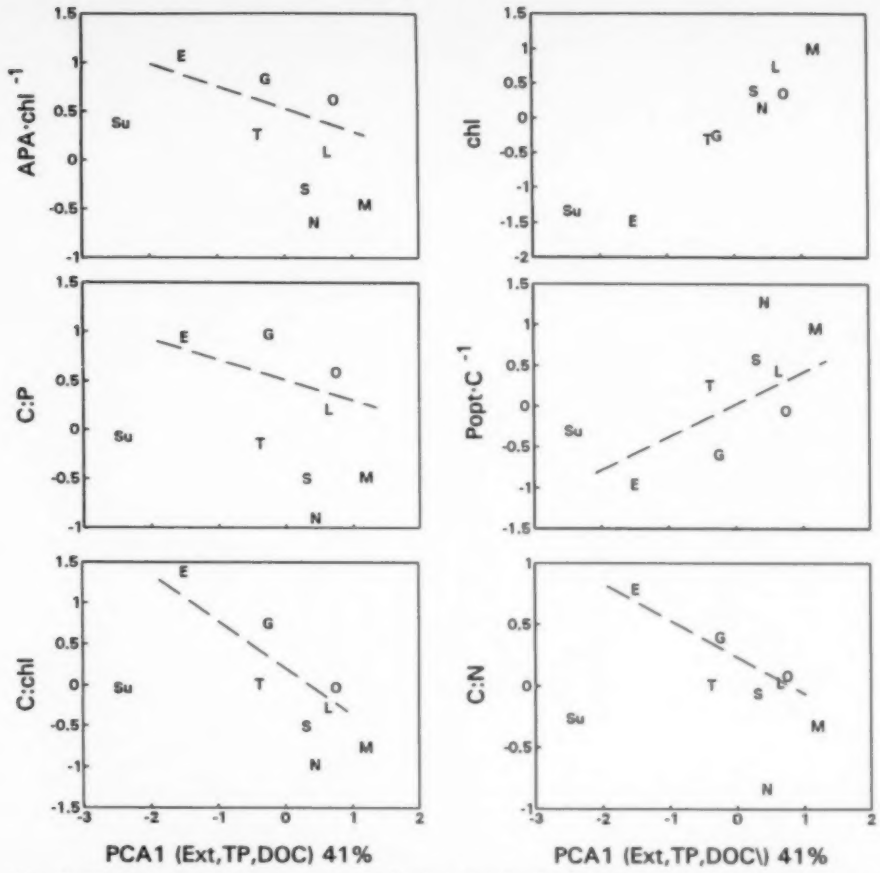


FIG. 7. Nutrient status and growth rate indicators (standardized means) plotted against the first principal components axis (PCA1). Dotted lines have been added to emphasize the separation between the smaller (E = Lake 373; G = Green Lake; O = Orange Lake) and larger lakes (see Table 1 for remaining lakes). Abbreviations are as in Table 3; units are as in Fig. 2.

mean TP concentrations (Table 4). In fact, the large lakes are not as P deficient as the small ones (Fig. 7). Nutrient status and growth rate estimators for each lake plotted against PC1 showed that the larger lakes are less nutrient deficient and have higher phytoplankton relative growth rates than smaller lakes with similar mean TP.

Deep mixing (Sterner 1990) and/or high light extinction (Hecky and Guildford 1984) in certain situations will result in light deficiency rather than nutrient deficiency. However, the deep mixed depth in Lake Superior usually did not lead to light deficiency, nor did the high light extinction coefficient in Musclow Lake. Other physical effects may explain the low nutrient deficiency in the large lakes. The thermocline is more stable in the small lakes than in the large ones (Fee et al. 1994). Fee et al. (1994) calculated eddy diffusivity coefficients for the NOLSS lakes and used vertical concentration gradients to show that little or no P is returned from below the epilimnion during the stratified period. Nevertheless, the large lakes have deeper and more turbulent mixed layers than the small lakes, which may result in more efficient retention of particles in the epilimnion (Fee et al. 1994); longer retention leads to improved nutrient recycling. Thus, lakes of different sizes having similar external inputs of P in the spring would have quite different fluxes of recycled P during the summer and, consequently, different degrees of P limitation.

The fact that a combination of chemical (PC1) and physical (PC2) variables correlate significantly with the nutrient status and growth rate variables is an artificial but useful finding. It is artificial because it is not really possible to separate chemical and physical variables in these systems. For example, we hypothesized that physical mixing depth influences P cycling, but it could be the cycling of P, rather than mixing depth, that directly influences nutrient status. Nonetheless, for this group of lakes, a combination of physical and chemical variables provided a useful classification because it described the combination of variables that best predicted the biological variables, and it showed that the factors predicting chl (algal biomass) did not account fully for variability in nutrient status (relative growth rate).

Application of Results from Small Systems to Large Systems

We have shown that the TP–chl relationship holds for all the lakes of the study. We have also shown that nutrient status, relative growth rate, and probably trophic performance

(Sterner et al. 1993; Hecky et al. 1993) of the study lakes are affected by size-related physical factors. Thus, models constructed to describe processes in large lakes, based on information from studies on small lakes that are highly nutrient deficient, must take into account differences imposed on lakes of different size by physical factors that affect within-lake nutrient regeneration. Processes known to be dependent on algal growth rates and algal quality include secondary production (Enright et al. 1986; Sterner et al. 1993), sensitivity to toxic metals (Creed et al. 1990; Twiss and Nalewajko 1992), and bioaccumulation of contaminants (Swackhamer and Skoglund 1993; Taylor et al. 1991). Nutrient status analyses yield information about phytoplankton growth rates, and so these analyses provide a means of scaling models of biological processes that depend on growth rate from small experimental lakes (Johnson and Vallentyne 1971) to large systems, including the Great Lakes where application of theory is most critical.

Acknowledgments

C. Anema coordinated the field sampling assisted by P. Cooley and C. Grose. The Freshwater Institute Analytical Chemistry Laboratory conducted the chemical analyses. Work on lakes Superior and Nipigon was supported by Great Lakes Action Plan (GLAP) funds and was facilitated by D. Pugh (Ontario Ministry of the Environment) and R. Salmon (Ontario Ministry of Natural Resources). D. Rosenberg, P. Healey, P. Ramlal, P. Campbell, and two anonymous reviewers provided useful comments on the manuscript.

References

AGUSTI, S., C.M. DUARTE, AND D.E. CANFIELD, JR. 1990. Phytoplankton abundance in Florida lakes: evidence for the frequent lack of nutrient limitation. Limnol. Oceanogr. 35: 181–188.

BOYCE, F.M. 1974. Some aspects of Great Lakes physics of importance to biological and chemical processes. J. Fish. Res. Board Can. 31: 689–730.

CANFIELD, D.E., JR., AND R.W. BACHMANN. 1981. Prediction of total phosphorus concentrations, chlorophyll a, and Secchi depths in natural and artificial lakes. Can. J. Fish. Aquat. Sci. 38: 414–423.

CREED, I.F., M. HAVAS, AND C.G. TRICK. 1990. Effects of arsenate on growth of nitrogen- and phosphorus-limited *Chlorella vulgaris* (Chlorophyceae) isolates. J. Phycol. 26: 641–650.

DILLON, P.J., AND F.H. RIGLER. 1974. The phoshporus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

DILLON, P.J., AND F.H. RIGLER. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J. Fish. Res. Board Can. 32: 1519–1531.

DROOP, M.R. 1968. Vitamin B12 and marine ecology. IV. The kinetics of uptake, growth, and inhibition in *Monochrysis lutheri*. J. Mar. Biol. Assoc. U.K. 48: 689–733.

DROOP, M.R. 1970. Vitamin B12 and marine ecology. V. Continuous culture and an approach to nutritional kinetics. Helgol. Wiss. Meeresunters. 20: 629–636.

ELLIOTT, J.M. 1983. Some methods for the statistical analysis of samples of benthic invertebrates. 2nd ed. Freshwater Biol. Assoc. Sci. Publ. 25: 160 p.

ENRIGHT, C.T., G.F. NEWKIRK, J.S. CRAIGIE, AND J.D. CASTELL. 1986. Growth of juvenille *Ostrea edulis* L. fed *Chaetoceros gracilis* Schutt of varied chemical composition. J. Exp. Mar. Biol. Ecol. 96: 15–26.

FEE, E.J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. Limnol. Oceanogr. 24: 401–416.

FEE, E.J. 1990. Computer programs for calculating *in situ* phytoplankton photosynthesis. Can. Tech. Rep. Fish. Aquat. Sci. 1740: 27 p.

FEE, E.J., AND R.E. HECKY. 1992. Introduction to the Northwest Ontario Lake Size Series (NOLSS). Can. J. Fish. Aquat. Sci. 49: 2434–2444.

FEE, E.J., R.E. HECKY, G.W. REGEHR, L.L. HENDZEL, AND P. WILKINSON. 1994. Effects of lake size on nutrient availability in the mixed layer during summer stratification. Can. J. Fish. Aquat. Sci. 51: 2756–2768.

FEE, E.J., R.E. HECKY, M.P. STAINTON, P. SANDBERG, L.L. HENDZEL, S.J. GUILDFORD, H.J. KLING, G.K. MCCULLOUGH, C. ANEMA, AND A. SALKI. 1989. Lake variability and climate research in Northwest Ontario: study design and 1985–1986 data from the Red Lake District. Can. Tech. Rep. Fish. Aquat. Sci. 1662: 39 p.

FEE, E.J., J.A. SHEARER, E.R. DEBRUYN, AND E.U. SCHINDLER. 1992. Effects of lake size on phytoplankton photosynthesis. Can. J. Fish. Aquat. Sci. 49: 2445–2459.

GUILDFORD, S.J., F.P. HEALEY, AND R.E. HECKY. 1987. Depression of primary productivity by humic matter and suspended sediment in limnocorral experiments at Southern Indian Lake, northern Manitoba. Can. J. Fish. Aquat. Sci. 44: 1408–1417.

HANNA, M., AND R.H. PETERS. 1991. Effect of sampling protocol on estimates of phosphorus and chlorophyll concentrations in lakes of low to moderate trophic status. Can. J. Fish. Aquat. Sci. 48: 1979–1986.

HARRIS, G.P. 1986. Phytoplankton ecology: structure, function and fluctuation. Chapman and Hall, London.

HEALEY, F.P. 1975. Physiological indicators of nutrient deficiency in algae. Can. Fish. Mar. Serv. Res. Dev. Tech. Rep. 585: 30 p.

HEALEY, F.P. 1977. Ammonium and urea uptake by some freshwater algae. Can. J. Bot. 55: 61–69.

HEALEY, F.P., AND L.L. HENDZEL. 1979a. Fluorometric measurements of alkaline phospahatase activity in algae. Freshwater Biol. 9: 429–439.

HEALEY, F.P., AND L.L. HENDZEL. 1979b. Indicators of phosphorus and nitrogen deficiency in five algae in culture. J. Fish. Res. Board Can. 36: 1364–1369.

HEALEY, F.P., AND L.L. HENDZEL. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Can. J. Fish. Aquat. Sci. 37: 442–453.

HECKY, R.E., P. CAMPBELL, AND L.L. HENDZEL. 1993. The stoichiometry of carbon, nitrogen and phosphorus in particulate matter of lakes and oceans. Limnol. Oceanogr. 38: 709–724.

HECKY, R.E., AND S.J. GUILDFORD. 1984. Primary productivity of Southern Indian Lake before, during and after impoundment and Churchill River diversion. Can. J. Fish. Aquat. Sci. 41: 591–604.

HECKY, R.E., AND P. KILHAM. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. Limnol. Oceanogr. 33: 796–822.

JOHNSON, W.E., AND J.R. VALLENTYNE. 1971. Rationale, background, and development of experimental lake studies in northwestern Ontario. J. Fish. Res. Board Can. 28: 123–128.

KLING, H.J., D.L. FINDLAY, AND J. KOMÁREK. 1994. *Aphanizomenon schindleri* sp.nov.: a new nostocacean cyanoprokaryote from the Experimental Lakes Area, northwestern Ontario. Can. J. Fish. Aquat. Sci. 51: 2267–2273.

LEAN, D.R.S. 1987. Overview of studies on the nutrient status of Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2042–2046.

LEAN, D.R.S., A.A. ABBOT, AND F.R. PICK. 1987. Phosphorus deficiency of Lake Ontario plankton. Can. J. Fish. Aquat. Sci. 44: 2069–2076.

LEAN, D.R.S., AND C. NALEWAJKO. 1979. Phosphorus turnover times and phosphorus demand in large and small lakes. Ergeb. Limnol. 13: 120–132.

LEGENDRE, L., AND S. DEMERS. 1984. Towards dynamic biological oceanography and limnology. Can. J. Fish. Aquat. Sci. 41: 2–19.

LEVASSEUR, M.E., P.J. HARRISON, B.R. HEIMDAL, AND J.C. THERRIAULT. 1990. Simultaneous nitrogen and silicate deficiency of a phytoplankton community in a coastal jet-front. Mar. Biol. 104: 329–338.

LOHMAN, K., AND J.C. PRISCU. 1992. Physiological indicators of nutrient deficiency in *Cladophora* (Chlorophyta) in the Clark Fork of the Columbia River, Montana. J. Phycol. 28: 443–448.

MAGNUSON, J.J., T.K. KRATZ, T.M. FROST, C.J. BOWSER, B.J. BENSON, AND R. NERO. 1991. Expanding the temporal and spatial scales of ecological research and comparison of divergent ecosystems: roles for LTER in the United States, p. 45–70. *In* P.G. Rissere [ed.] Long-term ecological research: an international perspective. Wiley, Sussex.

MARGALEF, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. Oceanol. Acta 1: 493–509.

MARSHALL, C.T., AND R.H. PETERS. 1989. General patterns in the seasonal development of chlorophyll *a* for temperate lakes. Limnol. Oceanogr. 34: 856–867.

MOLOT, L.A., AND P.J. DILLON. 1991. Nitrogen/phosphorus ratios and the prediction of chlorophyll in phosphorus-limited lakes in central Ontario. Can. J. Fish. Aquat. Sci. 48: 140–145.

NALEWAJKO, C., K. LEE, AND H. SHEAR. 1981. Phosphorus kinetics in Lake Superior: light intensity and phosphate uptake in algae. Can. J. Fish. Aquat. Sci. 38: 224–232.

PATALAS, K., AND A. SALKI. 1993. Spatial variation of crustacean plankton in lakes of different size. Can. J. Fish. Aquat. Sci. 50: 2626–2640.

PICK, F.R. 1987. Interpretation of alkaline phosphatase activity in Lake Ontario. Can. J. Fish. Aquat. Sci. 44: 2087–2094.

REYNOLDS, C.S. 1984. The ecology of freshwater phytoplankton. Cambridge University Press, London.

RILEY, E.T., AND E.E. PREPAS. 1985. Comparison of the phosphorus–chlorophyll relationship in mixed and stratified lakes. Can. J. Fish. Aquat. Sci. 42: 831–835.

SAKAMOTO, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. Arch. Hydrobiol. 62: 1–28.

SCHINDLER, D.W. 1977. The evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

SCHINDLER, D.W., K. BEATY, E.J. FEE, D. CRUIKSHANK, E. DEBRUYN, D. FINDLAY, G. LINSEY, J.A. SHEARER, M. STAINTON, AND M.A. TURNER. 1990. Effects of climate warming on lakes of the western boreal forest. Science (Wash., DC) 250: 967–970.

SMITH, V.H. 1991. Competition between consumers. Limnol. Oceanogr. 36: 820–823.

SOMMER, U. 1988. Does nutrient competition among phytoplankton occur *in situ*? Int. Ver. Theor. Angew. Limnol. Verh. 23: 707–712.

SOMMER, U. 1989. Nutrient status and nutrient competition of phytoplankton in a shallow, hypertrophic lake. Limnol. Oceanogr. 34: 1162–1173.

SOMMER, U. 1993. Phytoplankton competition in Plußsee: a field test of the resource-ratio hypothesis. Limnol. Oceanogr. 38: 838–845.

STAINTON, M.P., M.J. CAPEL, AND F.A.J. ARMSTRONG. 1977. The chemical analysis of fresh water. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25: 180 p.

STEEL, R.G.D., AND J.H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York.

STERNER, R.W. 1990. Lake morphology and light in the surface layer. Can. J. Fish. Aquat. Sci. 47: 687–692.

STERNER, R.W., D.D. HAGEMEIER, W.L. SMITH, AND R.F. SMITH. 1993. Phytoplankton nutrient limitation and food quality for *Daphnia*. Limnol. Oceanogr. 38: 857–871.

SUTTLE, C.A., W.P. COCHLAN, AND J.G. STOCKNER. 1991. Size-dependent ammonium and phosphate uptake, and N:P supply ratios in an oligotrophic lake. Can. J. Fish. Aquat. Sci. 48: 1226–1234.

SWACKHAMER, D.L., AND R.S. SKOGLUND. 1993. Bioaccumulation of PCBs by algae: kinetics versus equilibrium. Environ. Toxicol. Chem. 12: 831–838.

TAYLOR, W.D., J.H. CAREY, D.R.S. LEAN, AND D.J. MCQUEEN. 1991. Organochlorine concentrations in the plankton of lakes in southern Ontario and their relationship to plankton biomass. Can. J. Fish. Aquat. Sci. 48: 1960–1966.

TWISS, M.R., AND C. NALEWAJKO. 1992. Influence of phosphorus nutrition on copper toxicity to three strains of *Scenedesmus acutus* (Chlorophyceae). J. Phycol. 28: 291–298.

URABE, J., AND Y. WATANABE. 1992. Possibility of N or P limitation for planktonic cladocerans: an experimental test. Limnol. Oceanogr. 37: 244–251.

VAN DONK, E., AND S.S. KILHAM. 1990. Temperature effects on silicon- and phosphorus-limited growth and competitive interactions among three diatoms. J. Phycol. 26: 40–50.

WILKINSON, L. 1990. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, IL. 677 p.

Roles of Nutrients in Controlling Growth of Epilithon in Oligotrophic Lakes of Low Alkalinity[1]

Michael A. Turner

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

E. Todd Howell[2]

Institute for Environmental Studies, University of Toronto, Toronto, ON M5S 1A4, Canada

Gordon G.C. Robinson

Department of Botany, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

and Paul Campbell, Robert E. Hecky, and Eva U. Schindler

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Turner, M.A., E.T. Howell, G.G.C. Robinson, P. Campbell, R.E. Hecky, and E.U. Schindler. 1994. Roles of nutrients in controlling growth of epilithon in oligotrophic lakes of low alkalinity. Can. J. Fish. Aquat. Sci. 51: 2784–2793.

The ability of nutrients to control photosynthesis was compared in epilithon (the association on rock surfaces in the littoral zone) and phytoplankton of 13 low alkalinity lakes of the Experimental Lakes Area of northwestern Ontario. The study included (1) surveys of lakes varying in nutrient concentrations; (2) experimental additions to lakes of carbon and nitrogen (N), with or without phosphorus (P); and (3) experimental additions to lakes of sulfuric and nitric acids. Nutrient controls of planktonic and epilithic algal photosynthesis differed consistently. Phosphorus limited planktonic algal photosynthesis. In contrast, dissolved inorganic carbon (DIC) limited epilithic photosynthesis in both perturbed and unperturbed lakes because diffusive resistance kept the effective supply of DIC below the level needed for optimal growth. Epilithic photosynthesis was lowered when lake disturbances (e.g., acidification) reduced epilimnetic concentrations of DIC. Expected increases in atmospheric carbon dioxide can, therefore, differentially affect the littoral and pelagic food webs in low DIC lakes. Epilithic photosynthesis in all study lakes was unrelated to N or P availability despite apparent N and P deficiencies, based upon particulate nutrient ratios. Rates of epilithic respiration were, however, correlated with epilimnetic concentrations of inorganic N.

L'effet des éléments nutritifs sur le taux de photosynthèse a été comparé dans la flore épilithique (association végétale sur les surfaecs rocheuses de la zone riveraine) et dans le phytoplancton de 13 lacs faiblement alcalins de la région des lacs expérimentaux, dans le nord-ouest de l'Ontario. Le protocole de l'étude comprenait les éléments suivants : (1) repérage de lacs ayant diverses concentrations d'éléments nutritifs; (2) ajouts expérimentaux de carbone et d'azote (N) dans certains lacs, avec ou sans phosphore (P); et (3) ajouts expérimentaux d'acides sulfurique et nitrique dans certains lacs. L'effet des éléments nutritifs sur le taux de photosynthèse des algues planctoniques et épilithiques variait considérablement. Le phosphore constituait le facteur limitant dans le cas de la photosynthèese des algues planctoniques. Par ailleurs, le carbone inorganique dissous (CID) était le facteur limitantdans le cas de la photosynthèse des algues épilithiques dans les lacs soumis ou non à des perturbations parce que la résistance à la diffusion maintenait la réserve utile de CID sous le niveau requis pour une croissance optimale. La photosynthèse chez les algues épilithiques se trouvait réduite dans les lacs où les perturbations (acidification, p. ex.) avaient pour effet de diminuer les concentrations épilimniques de CID. L'accroissement attendu des taux de bioxyde de carbone atmosphérique peut donc influer différentiellement sur les réseaux alimentaires riverains et pélagiques des lacs à faible teneur en CID. Dans tous les lacs de l'étude, aucune relation n'a été observée entre le taux de photosynthèse des algues épilithiques et les concentrations de N ou de P assimilables malgré l'existence de carences apparentes en N et en P selon les ratios d'éléments nutritifs particulaires. Toutefois, les taux de respiration de la flore épilithique étaient corrélés avec les concentrations épilimniques de N inorganique.

Received August 5, 1993
Accepted July 12, 1994
(J12035)

Reçu le 5 août 1993
Accepté le 12 juillet 1994

[1]This paper is one of a series done in honor of the 25th anniversary of the Experimental Lakes Area.

[2]Present address: Surface Water Section, Environmental Monitoring and Reporting Branch, Ontario Ministry of the Environment and Energy, 125 Resources, Rd., Etobicoke, ON M4V 1P5, Canada.

Phosphorus (P) limits photosynthesis and biomass of phytoplankton in most inland lakes (Goldman et al. 1974; Schindler 1974) and periphyton in streams (Traaen 1978; Bothwell 1988, 1989). Although low P levels could saturate growth rates of thin films of stream periphyton, higher concentrations could stimulate areal accumulation of periphyton biomass (Bothwell 1988). The role of P in controlling growth of periphyton in lakes, however, is less clear. For example, P in lake water was correlated with benthic algal biomass on artificial substrata (Shortreed et al. 1984) and was shown to regulate growth of benthic filamentous green algae in the Great Lakes (Auer et al. 1983). In contrast, Fairchild and Sherman (1992) concluded that P was not the primary limiter of biomass developing on artificial substrata in 12 lakes ranging in total P from 0.2–1.3 μM. In other lake studies, development of periphytic biomass on artificial substrata was uncorrelated with ambient P levels (Stockner and Armstrong 1971; Evans and Stockner 1972; Ennis 1975) or correlated less well than did phytoplankton biomass (Cattaneo 1987), although there is some disagreement about this interpretation (e.g., see Ennis 1975; Shortreed et al. 1984).

The role of nitrogen (N) in controlling the growth of epilithon (the association on rock surfaces in the littoral zone) in lakes has been studied even less than that of P. Reuter et al. (1983, 1986) claimed that N regulated epilithic growth when concentrations were very low . This view is consistent with the occurrence of N_2-fixation (Reuter et al. 1983) and the importance of heterocystous cyanoprokaryotes[3] in epilithon (Loeb and Reuter 1981; Turner et al. 1987). Fairchild and Sherman (1992) concluded that N limitation was probable when the ratio of dissolved inorganic carbon (DIC) to N in lake water exceeded the Redfield (1958) atomic ratio of 6.6:1. This value is similar to the ratio of carbon (C) to N in phytoplankton (8.3:1) that Healey and Hendzel (1979) determined was the threshold for N deficiency.

Few lake studies have evaluated the ability of inorganic C to limit epilithic growth. The view "that inorganic carbon is not the major nutrient controlling algal growth in natural waters" (Goldman et al. 1974, p. 572) has been extended implicitly to benthic algal associations. Sheldon and Boylen (1975) argued that low-productivity epiphyton removed from *Potamogeton* in an oligotrophic lake was C limited. Turner et al. (1991) showed that photosynthesis of both epiphyton of *Eriocaulon* and epilithon in a low alkalinity lake was stimulated by additions of DIC. Fairchild and Sherman (1992) also concluded that photosynthesis of epilithon developing on artificial substrata in low alkalinity lakes was limited by DIC. Recent studies in acidified lakes have also indicated that DIC can be important to benthic photosynthesis (Turner et al. 1987, 1991; Fairchild et al. 1989; Fairchild and Sherman 1990, 1992). Photosynthesis of epilithon and epiphyton declined partly as a result of the reduced supply of DIC caused by the acidification-induced loss of bicarbonate. In contrast, there was no lessening in rates of phytoplankton photosynthesis (Shearer and DeBruyn 1986; Shearer et al. 1987).

The objective of this study was to reexamine the relative importance of C, N, and P as regulators of growth to epilithon and phytoplankton in lakes. Photosynthesis and respiration of epilithon were studied in experimental (acidified and eutrophied) and unperturbed lakes at the Experimental Lakes Area (ELA) in northwestern Ontario.

Methods

Study Area

The regional geology of the ELA (93°30′–94°00′W, 49°30′–49°45′N) was described by Brunskill and Schindler (1971) and by McCullough and Campbell (1993). The basic morphometric characteristics, experimental status, and years of seasonal monitoring of epilithic photosynthesis in the study lakes are described in Table 1. Water residence times exceeded 0.5 yr for all lakes except for Lake 938 (annual mean value = 0.07 yr). Pertinent epilimnetic chemistry (methods according to Stainton et al. 1977) of the study lakes is summarized in Tables 2 and 3.

Algal Associations Studied and Related Physical Restrictions

Undisturbed epilithon on natural substrata were studied in situ, as described below, for most of the experiments. Unshaded communities on rock surfaces of slope ≤10° were sampled at depths of 1–2 m (Turner et al. 1987). However, epilithon that developed on artificial substrata (acrylic and granite) in the Lake 226 whole-lake nutrient enrichment experiment (Turner 1981) also were used. These substrata, which had been placed in situ the year before sampling, were transferred by SCUBA diver from the lake bottom to an incubation chamber and returned to the laboratory.

Physical factors affect epilithic nutrient uptake in several ways: *(1) Water movement.* Nutrient uptake by epilithic biofilms is affected by boundary layer thickness, which is affected by water movement. As water movement increases, the boundary layer thins and nutrient uptake increases (Whitford and Schumacher 1961, 1964; Turner et al. 1991; Stevenson and Glover 1993). Excessive water movement can erode the biofilms, and reduce diffusive resistance and density-dependent effects. Static incubations of epilithon normally exposed to moving water may underestimate photosynthetic rates. In this study, the effects of water movement were standardized by using epilithon below the wave zone, and by using static incubations. *(2) Epilithon thickness.* Epilithon obtain nutrients from the overlying water column across a two-dimensional surface. Thus, as epilithic thickness increases, density-dependent effects can occur with regard to the diffusion of nutrients (Stevenson et al. 1991). Biofilm thickness was not controlled in this study. *(3) Epilithon shape.* Algae that form filamentous chains, or are stalked, usually escape the laminar flow conditions (and resulting slower nutrient uptake) associated with the surface of epilithon. This study pertains only to lentic epilithon up to several millimetres thick, which have boundary layer thicknesses of ~0.5 mm (Turner et al. 1991). *(4) Orientation of substrata.* Vertically oriented surfaces tend to accumulate less material (e.g., decaying algae) and have less nutrient recycling than surfaces of low slope. This study used epilithon on low-slope (<10°) substrata; water movement was nonerosional, so losses of nutrients were expected to be slow.

Metabolic Measurements

Net photosynthesis, rather than accrual of biomass, was used as a surrogate for growth in this study because changes in the availability of a limiting nutrient can modify algal

[3]We use the term "cyanoprokaryotes" as proposed by Kling et al. (1994) in lieu of blue-greens, blue-green algae, or cyanobacteria.

TABLE 1. Basic morphometric characteristics and experimental status of the study lakes during the investigation. The years are given during which epilithic photosynthesis was monitored. The sources of the morphometric data are (1) McCullough and Campbell (1993), (2) Beaty and Lyng (1989), and (3) D. Cruikshank (Department of Fisheries and Oceans, Winnipeg, MB, unpublished data).

Lake	Surface area (ha)	Mean depth (m)	Experimental status	Epilithic monitoring	Source
149	26.9	2.0	Reference	1992	1
226N	8.3	5.7	+ C, + N, + P	1976	2
226S, 1976	7.8	5.7	+ C, + N	1976	2
226S, 1989			Reference	1989	2
228	1677	55.4	Reference	1992	3
239	54.3	10.5	Reference	1981–92	2
302N	12.8	5.7	+ HNO_3	1981–84, 1986	2
302S	10.9	5.1	+ H_2SO_4	1981–92	2
305	52.0	15.1	Reference	1989	3
373	27.3	11.0	Reference	1992	1
375	18.7	11.6	Reference	1992	3
377	26.9	9.2	Reference	1992	1
382	36.9	5.8	Reference	1984, 1986	2
442	16.0	9.0	Reference	1992	1
938	19.2	2.0	Reference	1992	1

TABLE 2. Open-water means of epilimnetic chemistry and metabolism of epilithon and phytoplankton in four lakes of the Experimental Lakes Area. Units of measurement for dissolved inorganic carbon (DIC), NH_3, NO_3, and dissolved inorganic nitrogen (DIN) are μM, for epilithic maximum net photosynthesis (P_{max}) and respiration (R_d) are μmol $C \cdot m^{-2} \cdot h^{-1}$, and for optimum phytoplankton photosynthesis (P_{opt}) are μmol $C \cdot m^{-3} \cdot h^{-1}$.

Lake	Year	pH	DIC	NH_3	NO_3	DIN	P_{max}	R_d	P_{opt}
239	1981	7.0	156	0.5	0.3	0.9	315	105	498
239	1982	7.0	139	0.7	1.0	1.6	346	111	309
239	1983	7.0	144	1.4	1.0	2.4	396	126	309
239	1984	6.8	176	0.7	0.6	1.3	488	76	300
239	1985	6.8	146	3.6	0.9	4.4	358	57	446
239	1986	7.2	148	1.0	0.6	1.6	378	54	252
239	1987	7.2	143	1.2	0.4	1.6	342	64	289
239	1988	7.2	146	0.9	0.2	1.1	343	138	367
239	1989	7.2	153	0.4	0.5	0.9	431	84	330
239	1990	7.2	169	0.7	0.4	1.1	459	80	242
239	1991	7.1	173	0.4	0.6	1.1	481	9	235
382	1984	6.7	105	0.7	0.2	0.9	276	98	568
382	1986	6.9	86	2.1	0.4	2.5	305	72	336
302N	1981	6.6	80	0.4	0.1	0.6	256	62	731
302N	1982	6.5	53	1.1	17.1	18.3	218	110	811
302N	1983	6.3	46	2.4	23.0	25.6	164	154	550
302N	1984	6.2	51	2.1	43.3	44.0	196	144	792
302N	1986	6.1	20	3.4	49.8	53.5	97	174	634
302S	1981	6.8	75	0.5	0.1	0.6	231	74	637
302S	1982	6.4	62	0.8	0.6	1.4	214	121	436
302S	1983	5.9	32	1.9	1.8	3.7	176	191	424
302S	1984	5.7	31	2.5	0.7	3.3	98	181	621
302S	1985	5.5	29	4.0	1.7	5.8	88	222	575
302S	1986	5.0	17	4.4	1.0	5.4	58	366	362
302S	1987	5.0	32	4.6	1.0	5.6	133	371	748
302S	1988	4.6	28	13.3	1.1	14.3	46	333	504
302S	1989	4.6	26	21.8	1.6	23.5	45	403	732
302S	1990	4.5	21	29.1	2.5	31.6	−44	444	579
302S	1991	4.7	27	22.9	3.3	26.2	113	262	384

TABLE 3. Epilimnetic characteristics of Experimental Lakes Area lakes surveyed in 1989 and 1992. DIC = dissolved inorganic carbon, DIN = dissolved inorganic nitrogen, and P = total phosphorus; see text for additional details.

Code	Lake	Year	Day	Temp. (°C)	pH	DIC (μM)	DIN (μM)	P (μM)
1	224	1989	214	24	7.2	79		
2	226S	1989	221	25	7.2	86		
3	239	1989	219	23	7.2	138		
4	305	1989	212	22	7.5	115		
5	149	1992	202	24	7.2	171	9.9	0.29
6	228	1992	223	19	7.4	128	9.7	0.06
7	239	1992	189	17	7.2	147	0.6	0.16
8	239	1992	217	19	7.3	149	1.0	0.16
9	302S[a]	1992	191	18	4.8	23	16.6	0.29
10	302S[a]	1992	219	20	4.8	17	10.2	0.32
11	373[b]	1992	197	20	7.4	178	0.2	0.16
12	375	1992	199	19	7.5	479	0.5	0.16
13	377	1992	195	19	7.0	126	0.2	0.26
14	442[b]	1992	196	20	7.0	126	0.2	0.27
15	938[c]	1992	203	19	7.1	203	0.2	0.23

[a]Experimentally acidified lake.
[b]Based on profile information.
[c]Riverine in character.

growth rates without altering final yields (O'Brien 1972). Similarly, changes in epilithic biomass provide little information about nutrient limitation of growth (Fairchild and Sherman 1992). Areal rates of epilithic photosynthesis and volumetric rates of planktonic photosynthesis were measured recognizing that these measures incorporate changes in both algal biomass and biomass-specific photosynthesis. Although chlorophyll concentrations are often used to calculate biomass-specific rates of phytoplankton photosynthesis, such an approach is unreliable for calculating benthic biomass-specific photosynthesis, so photosynthesis was not expressed per unit of chlorophyll.

Analysis of epilithic metabolism mainly involved measurement of the change in DIC concentration in water overlying enclosed samples. Community dark respiration (R_d) was estimated by measuring efflux of DIC in samples enclosed in the dark. Photosynthesis-irradiance responses were generated by manipulating the amount of light available to other samples in situ. From these, the maximum areal rate of net photosynthesis (P_{max}) was estimated (Turner et al. 1991). Photosynthesis was also estimated by measuring changes in DI^{14}C in water overlying epilithic samples during the Lake 226 study. For the purposes of this study, ^{14}C uptake by epilithon or phytoplankton at saturating irradiances was interpreted as being P_{max}. Estimation of gross photosynthesis by adjusting P_{max} for R_d was avoided because this frequently used technique is biased (Graham and Turner 1987), especially when R_d is large relative to P_{max}.

The dependence of P_{max} on DIC (see below) was not an artifact of lowered DIC concentrations during the incubation assays. Photosynthesis of Lake 239 epilithon at saturating irradiances was linear for at least 4 h (Turner et al. 1983, 1987). In spite of these findings, incubation times were shortened to 1.5–2 h to avoid artificial limitation.

Lake 938 presented a special case because of water flow in this riverine lake, even at depths of ~2 m. Static incubations are inappropriate for epilithon in flowing water because epilithic boundary layers are naturally thinner than those found in static chambers (Turner et al. 1991). Thus, static incubations caused unnaturally thick boundary layers around Lake 938 epilithon, resulting in an underestimate of in situ rates (Turner et al. 1991).

Phytoplankton sampling techniques are described by Shearer (1978). Laboratory procedures for measurement of phytoplankton photosynthesis prior to 1986 (^{14}C uptake) are described by Shearer et al. (1985). Subsequent to 1986, only a single addition of ^{14}C was mixed into the phytoplankton sample, which was then subsampled. Also, a different type of incubator was used in 1992.

Lake 226 Nutrient Enrichment Experiment

The Lake 226 whole-lake experiment was designed to test the role of P in controlling algal growth when C and N were also supplied. The north (N) and south (S) basins of the lake were separated, and both were enriched with sucrose and nitrate (NO_3) at an annual rate of 4 g C·m^{-2} and 2 g N·m^{-2} (Schindler 1974; Cruikshank 1984). Phosphoric acid was added to Lake 226N only, at an annual rate of 0.3 g P·m^{-2}. Planktonic and epilithic photosynthesis were compared from May to October of 1976; the ratio of maximum rates of photosynthesis in Lake 226N to those in Lake 226S was used to simplify comparison of epilithic and planktonic results. The mean epilimnetic concentrations (μM) of DIC, DIN (ammonia [NH_3] plus NO_3, excluding nitrite which is negligible), and total P were 130, 7.5, and 0.26 in Lake 226S, and 116, 2.2, and 0.68 in Lake 226N during the open-water season of 1976. Total P, although including fractions unavailable to benthic algae, is used as the measure of available P in the absence of another more suitable measure of available P in these lakes (Schindler et al. 1973).

Normal incubation procedures were modified for Lake 226N samples, because epilimnetic DIC declined markedly to a minimum of 17 μM in July, despite the added C. Lake 226N samples were thus occasionally supplemented with sodium bicarbonate to achieve DIC levels similar to those in Lake 226S. The important role of inorganic C to

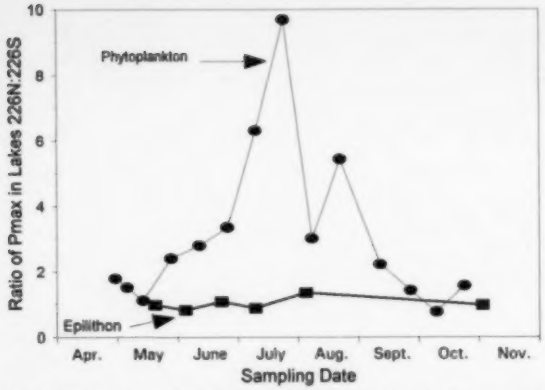


FIG. 1. Ratio of maximum rates of photosynthesis in Lake 226N / Lake 226S of phytoplankton (P_{opt}) and epilithon (P_{max}) during 1976.

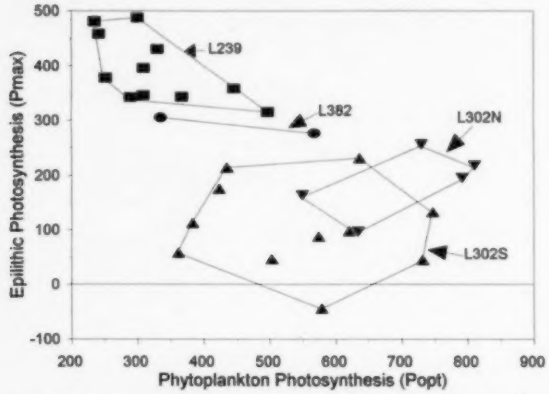


FIG. 2. Relationship between epilithic and planktonic photosynthesis. Units of measurement for epilithic maximum net photosynthesis (P_{max}) are μmol C·m^{-2}·h^{-1} and for optimum phytoplankton photosynthesis (Popt) are μmol C·m^{-3}·h^{-1}. Open-water mean rates in the four study lakes are shown for the periods described in Table 1. Means for specific lakes are enclosed within envelopes.

benthic photosynthesis was unrecognized in 1976, so epilithic rates measured in Lake 226N samples potentially overestimated in situ rates.

Epilithon in Lake 226N may have been P enriched but no information on P concentrations in epilithon was collected during the experiment. Average concentrations of P per unit of organic matter, however, were higher in the epilithon of P-fertilized Lake 227 than in nearby unfertilized lakes (239, 240, and 305). In contrast, areal epilithic concentrations of P were unrelated to water-column concentrations (Stockner and Armstrong 1971).

Time Series and Midsummer Surveys of Algal Metabolism

Rates of epilithic photosynthesis were monitored for several years in four lakes (239, 302N, 302S, and 382; details provided in Table 2). The epilithon of four lakes (224, 226S, 239, and 305) that covered a range of P concentrations was also examined during late July and early August of 1989. This period represented the annually dominant algal assemblage (Turner

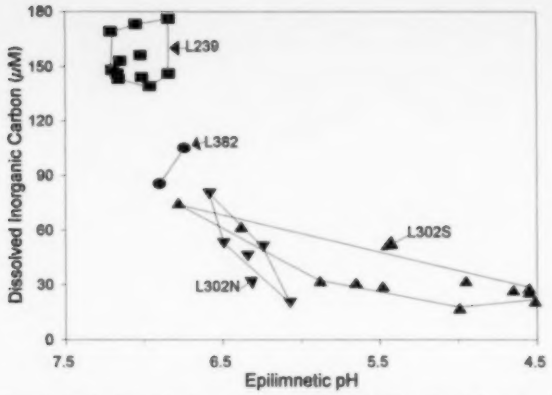


FIG. 3. Relationship between epilimnetic dissolved inorganic carbon (DIC) and pH. Open-water means of epilimnetic DIC are shown for the four study lakes for the periods described in Table 1. Means for specific lakes are enclosed within envelopes.

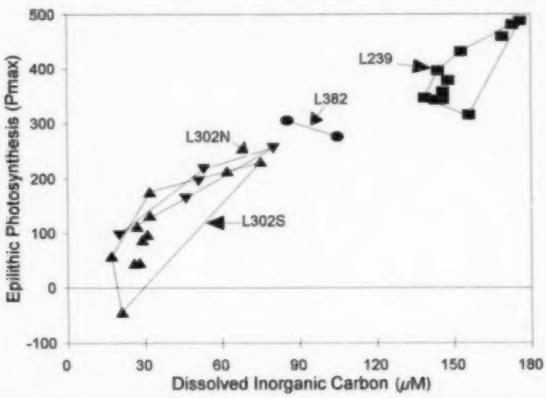


FIG. 4. Mean annual maximum rates of net photosynthesis in epilithon as a function of epilimnetic dissolved inorganic carbon. Units of measurement for epilithic maximum net photosynthesis (P_{max}) are μmol C·m^{-2}·h^{-1}. Means for specific lakes are enclosed within envelopes.

et al. 1991), and rates of photosynthesis and respiration of natural epilithon probably were near their annual maxima (Turner et al. 1995a). In contrast, rates of photosynthesis of acidified epilithon (Lake 302S) were probably at their annual minimum in July and August.

A second survey of epilithic metabolism was conducted during July and early August of 1992 on a larger suite of lakes (149, 228, 239, 302S, 373, 375, 377, 442, and 938) that extended the range of epilimnetic chemistry conditions examined. Dissolved inorganic C ranged from 12 to 480 μM, DIN from 0.2 to 17 μM, and total P from 0.06 to 0.32 μM (Table 3). All lakes were unperturbed except for Lake 302S (Table 1). Lakes 239 and 302S were sampled twice during this period.

Results

Lake 226 Nutrient Enrichment Experiment

The responses of the two algal associations in Lake 226 to P enrichment were markedly different (Fig. 1). Phytoplankton photosynthesis was accelerated by the addition of P to

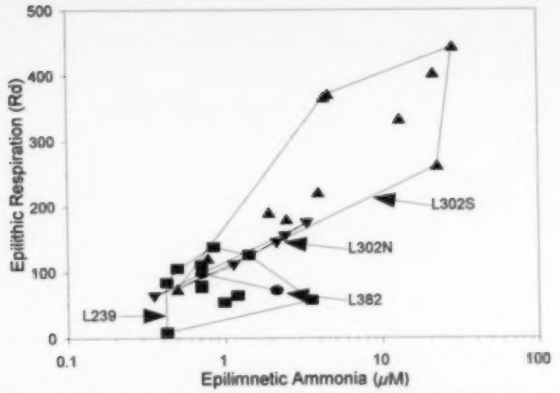


FIG. 5. Mean open-water values of epilithic dark respiration (R_d) as a function of epilimnetic mean concentrations of ammonia in four study lakes (see Fig. 3 for details). Units of measurement for R_d are μmol $C \cdot m^{-2} \cdot h^{-1}$. Means for specific lakes are enclosed within envelopes.

Lake 226N on 13 of 14 occasions. The mean ratio of maximum rates of phytoplankton photosynthesis in Lake 226N / Lake 226S was 3.1 ± 2.5 (mean ± SD), with a maximum of 9.7 in midsummer. Epilithic P_{max}, in contrast, was similar in magnitude in the two basins; the mean ratio of maximum epilithic rates was 1.0 ± 0.2. The supplementation of Lake 226N epilithic samples with DIC prior to incubations would have raised measured rates; hence, the ratio of Lake 226N / Lake 226S in situ rates probably would have been lower.

The irradiance parameter (α) for epilithon, derived using Smith's (1936) photosynthesis-irradiance relationship, was also independent of P levels. The mean values of α for May 17 – July 7 were similar between lakes (N/S = 1.1 ± 0.4, $n = 5$). Therefore, potential shading effects by phytoplankton did not cause a large systematic change in α of epilithon.

Epilithic dark respiration also was unaffected by P addition. Mean respiration rates for the period 17 May – 7 July were 200 ± 41 (mean ± SE, $n = 5$ means) and 180 ± 24 μmol $C \cdot m^{-2} \cdot h^{-1}$ for Lakes 226N and 226S, respectively.

Time Series in Acidified and Reference Lakes

Annual mean rates of epilithic and planktonic photosynthesis were not positively related when compared in the four study lakes (Fig. 2). The simple linear correlation was nonsignificant in each of acidified Lakes 302N and 302S ($P \gg 0.1$), but was actually negative in circumneutral Lake 239 ($r = -0.63$, $n = 11$, $P < 0.05$).

Epilithic photosynthesis correlated positively with pH (i.e., declined with acidification) in these four lakes (Table 2; $r = 0.89$, $n = 29$, $P \ll 0.01$). Dissolved inorganic C concentrations declined strongly in Lakes 302N and 302S during their acidification (Fig. 3); the major decline occurred as pH decreased from 7 to 6, as bicarbonate was lost. Rates of epilithic photosynthesis were thus positively related to ambient DIC (Fig. 4; $r = 0.95$, $n = 29$, $P \ll 0.01$), and declined with acidification. In contrast, planktonic photosynthesis was correlated negatively with decreasing DIC ($r = -0.65$, $n = 29$, $P \ll 0.01$), and increased with acidification.

TABLE 4. Survey of metabolism of phytoplankton and epilithon in several Experimental Lakes Area lakes during 1989 and 1992. Codes correspond to those in Table 3. Phytoplankton were also sampled at other times as noted. Units of measurement for phytoplankton optimum photosynthesis (P_{opt}) are μmol $C \cdot m^{-3} \cdot h^{-1}$, for epilithic maximum net photosynthesis (P_{max}) and respiration (R_d) are μmol $C \cdot m^{-2} \cdot h^{-1}$, and for epilithic carbon (C), nitrogen (N), and phosphorus (P) are μmol $\cdot cm^{-2}$.

Code	Lake	P_{opt}[a]	P_{max}	R_d	C	N	P
1	224	237[b]	418	233	484	36	0.47
2	226S	390[c]	439	188	221	17	0.25
3	239	300[d]	564	116	293	20	0.35
4	305	174[e]	585	146	233		0.28
5	149	1214[f]	740	310	259	23	0.25
6	228	108	459	221	219	19	0.19
7	239	327[g]	436	−24	390	26	0.51
8	239	308[h]	493	−9	331	22	0.42
9	302S	704	21	367	167	14	0.31
10	302S	424	38	352	141	12	0.31
11	373	164	875	76	258	18	0.28
12	375	300	1662	−65	209	13	0.21
13	377	296	550	24	226	15	0.23
14	442	327	423	46	125	9	0.13
15	938	380[i]	521	5	149	11	0.28

[a]Phytoplankton P_{opt} was determined as the average of several samplings.
[b]11 July and 8 August 1989.
[c]19 July and 17 August 1989.
[d]24 and 31 July, 10 August 1989.
[e]27 July and 8 August 1982; 10 July, 7 and 29 August 1984; 15 July and 12 August 1985; 30 July and 25 August 1986.
[f]14 and 28 July 1992.
[g]29 June and 13 July 1992.
[h]27 July and 10 August 1992.
[i]14 and 21 July 1992.

Rates of epilithic respiration correlated positively with increasing acidification (Table 2; $r = -0.93$, $n = 29$, $P \ll 0.01$). There was also a significant but weaker positive correlation between respiration and NH_3 concentrations (Table 2; $r = 0.77$, $n = 29$, $P \ll 0.01$), and with the logarithm of NH_3 concentrations (Fig. 5).

Midsummer Surveys of Algal Metabolism

The relationship of photosynthetic rates with DIC concentrations also differed between algal communities during the midsummer surveys (Table 4). Maximum rates of phytoplankton photosynthesis were unrelated to DIC in both 1989 ($r = 0.11$, $n = 4$) and 1992 ($r = 0.07$, $n = 11$). In contrast, epilithic photosynthesis was related positively and linearly to DIC in both surveys. The maximum in situ rates of epilithic photosynthesis in four circumneutral lakes (239, 226S, 224, and 305) were related positively to DIC in 1989 (Fig. 6), but the relationship was not statistically significant, probably because of the low number of observations ($r = 0.90$, $n = 4$, $P \sim 0.1$). Photosynthesis was also linearly related to ambient DIC in 1992 (Fig. 6; $r = 0.96$, $n = 11$, $P \ll 0.01$). The relationship between epilithic photosynthesis and DIC may have become nonlinear at higher concentrations, but additional observations are needed to confirm this point. Measured rates of photosynthesis in riverine Lake 938 were lower than those in lakes of similar DIC (Fig. 6), as expected (see Methods).

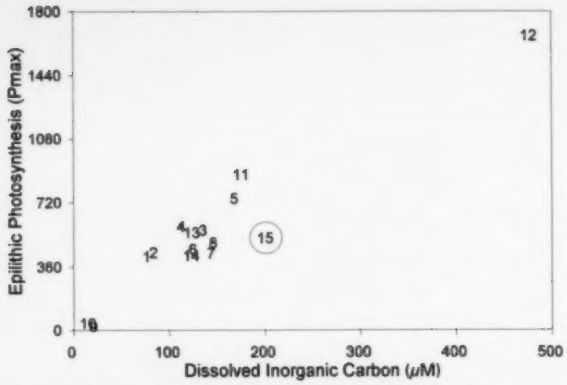


FIG. 6. Maximum rate of net photosynthesis of epilithon (P_{max}) in lakes as a function of dissolved inorganic carbon during surveys in July and August of 1989 and 1992; see Table 3 for lake codes. Units of measurement for P_{max} are μmol $C \cdot m^{-2} \cdot h^{-1}$. The value for riverine Lake 938 (circled) is probably unnaturally low as described in the text.

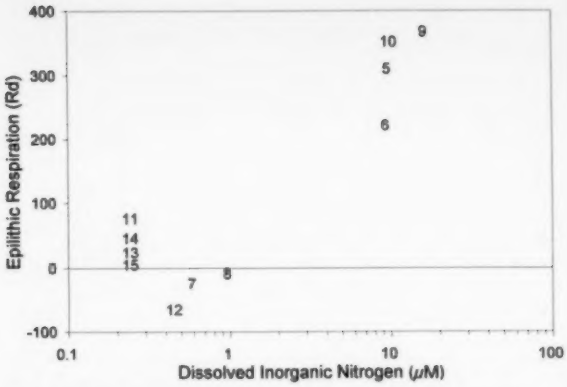


FIG. 7. Relationship between rates of dark respiration (R_d) in epilithon and epilimnetic concentrations of dissolved inorganic nitrogen in several lakes during July and August 1992; see Table 3 for lake codes. Units of measurement for epilithic R_d are μmol $C \cdot m^{-2} \cdot h^{-1}$.

Epilithic P_{max} was unrelated to epilimnetic total P concentrations (Table 4). Lake 305 epilithic P_{max} rates were the highest seen in the 1989 survey, yet Lake 305 is ultraoligotrophic, and has typical planktonic chlorophyll levels of <1 $\mu g \cdot L^{-1}$. Epilithic photosynthesis was also unrelated to epilimnetic P ($r = -0.41$, $n = 11$, $P \geq 0.05$) in 1992. Epilithic photosynthesis was similarly unrelated to the epilithic concentration of P ($r = -0.24$, $n = 15$, $P \geq 0.05$) or to the epilithic ratio of N/P ($r = 0.26$, $n = 14$, $P \geq 0.05$), in combined 1989 and 1992 observations. Unlike epilithic photosynthesis, phytoplankton photosynthesis was positively related to prevailing epilimnetic concentrations of P ($r = 0.61$, $n = 11$, $P < 0.05$).

Epilithic respiration was positively related to ambient levels of DIN (Fig. 7; $r = 0.94$, $n = 11$, $P < 0.01$). Although respiration was most rapid in acidified Lake 302S, surprisingly high rates also were measured in circumneutral Lakes 149 and 228. Dissolved inorganic N was dominated by NH_3 in shallow mesotrophic Lake 149, and by NO_3 in deep ultraoligotrophic Lake 228.

Discussion

Each of the three investigations confirmed different roles of nutrients in controlling photosynthesis of lentic epilithon and phytoplankton. The investigations of epilithic N and P deficiency excluded short-term enrichment experiments because the approach of detecting deficiencies by measuring algal responses to short-term N and P additions is unreliable (Healey 1973, 1979).

Inorganic Carbon Limitation of Lentic Epilithon

Rates of photosynthesis in epilithon of both experimental and unperturbed lakes were limited by DIC in the overlying water. Photosynthesis of epilithon declined (Fig. 4) as DIC decreased with acidification (Fig. 3), and was most rapid in lakes with high DIC (Fig. 6). These observations are consistent with the stimulation of photosynthesis of both epilithon and epiphyton by experimental additions of DIC in circumneutral lakes with DIC < 200 μM (Turner et al. 1987, 1991). The occurrence of much higher rates of periphytic photosynthesis in high DIC lakes (e.g., Borax Lake, California; Wetzel 1964) than in the low-DIC ELA lakes reinforces the importance of DIC.

Different types of C limitation occur in benthic associations. For example, C limitation in acidic lakes may be attributable simply to concentrations of DIC that are below the DIC compensation point of many algae (Birmingham and Colman 1979). Phytoplankton photosynthesis is unaffected by the low DIC of acidification, so planktonic taxa are capable of efficient DIC use at low concentrations. In contrast, epilithic limitation is sufficiently intense that even the most efficient DIC users are limited. Carbon limitation occurred in this study both in acidified epilithon (Fig. 4), where the number of algal taxa declined with acidification (Turner et al. 1995c), and in unperturbed associations.

Diffusive resistance can keep the effective supply of DIC below the level observed to limit growth even in lakes where concentrations would otherwise exceed the threshold level of individual taxa. Carbon supply to periphyton is restricted by boundary layers, as substantiated by isotopic fractionation of ^{13}C in both epilithon and epiphyton compared to phytoplankton (R.H. Hesslein and M.A. Turner, Department of Fisheries and Oceans, Winnipeg, MB, unpublished data).

If DIC directly affects rates of epilithic photosynthesis, then seasonal changes in DIC should cause corresponding changes in photosynthesis. This was seen at ELA in acidic lakes but not in circumneutral lakes containing more bicarbonate (Turner et al. 1995b). The effects of temporal changes of DIC in circumneutral lakes were likely dampened by temperature effects (Turner et al. 1995c). Thus, relatively small changes in DIC concentrations were uncorrelated, or were negatively correlated, with changes in photosynthesis of circumneutral epilithon. Several compensatory processes may have increased as a function of higher temperatures, including active algal uptake, passive diffusion of carbon dioxide (CO_2), and the efficiency of the photosynthetic process itself.

Phosphorus is Generally in Sufficient Supply for Lentic Epilithon

Although the majority of the ELA study lakes were oligotrophic, rates of epilithic photosynthesis were unrelated to either epilimnetic or epilithic concentrations of P (Table 4).

This was true even in ultraoligotrophic Lake 228, and during the Lake 226 P-addition experiment (Fig. 1). In contrast, phytoplankton photosynthesis was related directly to epilimnetic P. A similar dichotomy between phytoplankton and periphyton was observed in response to additions of sewage to Lake Mikolajskie, Poland (Chróst and Sikorska 1976) and nutrients to subarctic lakes in Sweden (Persson et al. 1977).

The notion of P sufficiency in lentic epilithic habitats of low slope is consistent with several related concepts. The littoral zone is a site of accumulation and degradation of materials (Castenholz 1960). That is, decomposing cells in the epilithic matrix provide P for growth by viable cells, making the effective residence time of P (and other nutrients) much longer in the littoral than in the pelagic zone. Confer (1972) and Jackson and Jackson (1972) also concluded that periphyton can have greater P trapping ability than an equivalent biomass of phytoplankton.

The hypothesis of P sufficiency in epilithon of oligotrophic lakes cannot be generalized to all epilithon. For example, P limitation in lotic epilithon has been well documented (Traaen 1978; Bothwell 1988, 1989) and is caused by several factors. First, erosional forces of water movement thin the epilithic matrix, thereby reducing the effective residence time of P. Second, water movement also reduces diffusive resistance to CO_2 uptake and enhances the uptake potential for all nutrients. These considerations also apply to lentic epiphyton and epilithon developing on vertical surfaces, especially where water movement is high.

Lentic epilithon can be P limited when DIC is high. For example, P controls the growth of the filamentous green algae, *Cladophora* and *Ulothrix*, in the high DIC environment of the Great Lakes (Auer et al. 1983). High DIC effectively diminishes the resistance to diffusion of DIC into epilithon, and enhances limitation of epilithon by other nutrients such as P. In addition, the considerations described for streams will also apply to benthic algae such as *Ulothrix*, which grows in the shallows of lakes, a region of considerable water movement.

Roles of Nitrogen

Nitrogen, like P, played a lesser role than C as a limiter of epilithic photosynthesis. Photosynthesis in Lake 302N declined despite increased NO_3 concentrations caused by nitric acid additions (Table 2). Similarly, photosynthetic rates in Lake 302S declined during sulfuric acid additions despite strongly elevated concentrations of ammonium (NH_4) (Table 2). Rates in Lakes 149 and 228, which had high DIN (Table 3), were consistent with values expected based on the dependency of P_{max} on DIC (Fig. 6). Furthermore, rates of epilithic photosynthesis in Lake 226S were similar to those seen in lakes of much lower DIN despite the experimental addition of NO_3. For example, the 1976 July mean value for P_{max} in Lake 226S (~560 $\mu mol \cdot m^{-2} \cdot h^{-1}$ at ~125 μM DIC) coincides with the 1989- and 1992-derived relationships of P_{max} with DIC (Fig. 6).

Heterocystous cyanoprokaryotes often are important components of epilithon (Persson et al. 1977; Loeb and Reuter 1981; Reuter et al. 1983; Turner et al. 1987, 1991), and as a result, N_2-fixation by benthic cyanoprokaryotes may allow epilithon to at least partly overcome N limitation (Schindler 1977; Reuter et al. 1983). Furthermore, N_2-fixation is inducible as a result of experimental P-only additions (Persson et al. 1977). This capacity will decline with acidification because heterocystous cyanoprokaryotes are lost below pH 5 (Turner et al. 1991, 1995c); however, NH_4 concentrations increase with acidification (Rudd et al. 1988, 1990), diminishing the need for supplemental N.

An Unexpected Role for Nitrogen?

The association of high rates of epilithic respiration with high ambient concentrations of DIN may indicate an unexpected role for inorganic N in controlling benthic algal growth. Rates of epilithic respiration increased as concentrations of NH_4 increased with acidification during the time-series studies of lakes 302N and 302S (Fig. 5). Although this correlation may have been caused by acidification (reviewed by Turner et al. 1991), the relationship was also found in circumneutral lakes 149 and 228, which had high rates of respiration (Fig. 7) and high DIN (Table 3). Moreover, the dominant forms of DIN were different. It can be concluded that high NH_3 in shallow Lake 149 is a result of respiration rather than its cause. This is more difficult to argue when NO_3 is the dominant form in deep Lake 228, although oxidation of NH_3 may occur more effectively in Lake 228; additional research is needed to resolve this matter. Although the cause of the apparent relationship between DIN and epilithic respiration is unknown, the relationship is consistent with the observation that increasing N/C in decomposing aquatic materials stimulates rates of decomposition (Godshalk and Wetzel 1978; Blackburn and Henriksen 1983).

Past and Future Aquatic Perturbations

Eutrophication

As a result of the contrasting conditions of P limitation between littoral and pelagic algal associations in low DIC lakes, eutrophication or increased P loading in such lakes favors energy flow in the pelagic zone. The relative importance of epilithic photosynthesis in these lakes should increase as external P loading declines with the introduction of P control measures.

Epilithon should also decline in importance relative to phytoplankton as a lake is eutrophied because CO_2 utilization by phytoplankton will decrease available DIC. Shading by phytoplankton can also decrease benthic photosynthetic potential. For example, there was no change in effectiveness of epilithon at low irradiances (i.e., α was unchanged) despite more severe attenuation of light in the epilimnion of the P-addition basin of Lake 226 than in the control (Fee et al. 1991).

Acidification

Carbon limitation increased in acidified epilithon and epiphyton of lakes (Turner et al. 1987, 1991; Fairchild and Sherman 1990; Fig. 2) and streams with pH ≤ 6 (Mulholland et al. 1986). This is consistent with the major decline seen in DIC with acidification (Fig. 3). The absence of carbonate in acid lake water also eliminated any possibility of chemical enhancement of CO_2 transport across the atmosphere–epilimnion interface, such as occurs in eutrophic lakes (Schindler 1975).

Even bloom-forming, filamentous green algae (e.g., Zygnematales) can be CO_2 limited (Howell et al. 1990; Turner et al. 1995a). Although their success in acid lakes can be attributed partly to their ability to sequester CO_2 at the low concentrations characteristic of acid lakes (Turner et al.

1991; G.G.C. Robinson, unpublished data), concentrations can be low enough to limit their rate of CO_2 uptake (Turner et al. 1995a).

Unfortunately, the importance of inorganic C to benthic algal associations can also induce artifacts in experimental studies of stream acidification. Acidification of circumneutral stream water without atmospheric equilibration can cause unnaturally supersaturated CO_2 solutions (e.g., Parent et al. 1986; Planas et al. 1989). As a result, researchers may cause unusually high growth rates, and distort the algal composition of the experimental communities.

Increased atmospheric carbon dioxide

Aqueous CO_2 concentrations have increased since the beginning of the industrial age (Hutchinson 1957), and with increases in atmospheric CO_2 expected to continue (Hengeveld 1991), levels should increase further in lake epilimnia. Although anticipated increases in water temperature will lower CO_2 solubility, expected increases in atmospheric CO_2 levels should overwhelm this effect. Increased aqueous CO_2 should therefore stimulate epilithic photosynthesis (Fig. 6), which is presently limited in low DIC lakes, without affecting phytoplankton photosynthesis, which is not limited by DIC. This differential response may already have begun.

The combination of acidification and increased atmospheric CO_2 could have even greater biological consequences. Filamentous green algal associations already proliferate in acidic lakes in spite of demonstrated CO_2 limitation (Turner et al. 1995a). Their growth could be substantially increased with higher CO_2. Their further proliferation could reduce the aesthetic and recreational value of lakes, and lead to important changes in several biological, chemical, and physical properties of the acidified littoral zones (Turner et al. 1995b). It will be important to test the hypotheses that littoral zone productivity will increase relative to the pelagic zone as atmospheric CO_2 levels increase, and that acidified lakes will be most sensitive to this increase.

Acknowledgments

Funding was provided by the Department of Fisheries and Oceans, Canada. E.T. Howell was supported by a Natural Sciences and Engineering Research Council Shield postdoctoral scholarship during his participation in this study. Technical assistance was supplied by R. Graham, M. Summerby, L. Sigurdson, L. Kirkendale, N. Strange, and B. Townsend. E. Fee provided the phytoplankton and epilimnetic chemistry data for Lake 228 in 1992. D. Cruikshank and his staff facilitated logistics for the whole-lake experiments. The chemical analyses reported in Tables 2 and 3 were done by M. Stainton, R. Schade, and their staff. The manuscript was improved by the constructive reviews of M. Bothwell, G. Fairchild, B. Hann, F. Healey, N. Kenkel, D. Schindler, and especially D. Rosenberg. Elements of this work were originally part of a Ph.D. thesis by M.A. Turner at the University of Manitoba.

References

Auer, M.T., J.M. Graham, L.E. Graham, and J.A. Kranzfelder. 1983. Factors regulating the spatial and temporal distribution of *Cladophora* and *Ulothrix* in the Laurentian Great Lakes, p. 135–145. *In* R.G. Wetzel [ed.] Periphyton of freshwater ecosystems. Dr. W. Junk, The Hague, The Netherlands.

Beaty, K.G., and M.E. Lyng. 1989. Hydrometeorological data for the Experimental Lakes Area, northwestern Ontario, 1982 to 1987. Can. Data. Rep. Fish. Aquat. Sci. 759: 280 p.

Birmingham, B.C., and B. Colman. 1979. Measurement of carbon dioxide compensation points of freshwater algae. Plant Physiol. 64: 892–895.

Blackburn, T.H., and K. Henriksen. 1983. Nitrogen cycling in different types of sediments from Danish waters. Limnol. Oceanogr. 28: 477–493.

Bothwell, M.L. 1988. Growth rate responses of lotic periphytic diatoms to experimental phosphorus enrichment: the influence of temperature and light. Can. J. Fish. Aquat. Sci. 45: 261–270.

Bothwell, M.L. 1989. Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. Can. J. Fish. Aquat. Sci. 46: 1293–1301.

Brunskill, G.J., and D.W. Schindler. 1971. Geography and bathymetry of selected lake basins, Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 139–155.

Castenholz, R.W. 1960. Seasonal changes in the attached algae of freshwater and saline lakes in the lower Grand Coulee, Washington. Limnol. Oceanogr. 5: 1–28.

Cattaneo, A. 1987. Periphyton in lakes of different trophy. Can. J. Fish. Aquat. Sci. 44: 296–303.

Chróst, R. J., and U. Sikorska. 1976. The effect of pollution on photosynthetic activity of algae and physiological activity of bacteria in lakes. Pol. Arch. Hydrobiol. 23: 357–364.

Confer, J.L. 1972. Interrelations among plankton, attached algae, and the phosphorus cycle in artificial open systems. Ecol. Monogr. 42: 1–23.

Cruikshank, D.R. 1984. Whole lake chemical additions in the Experimental Lakes Area. 1969–1983. Can. Data Rep. Fish. Aquat. Sci. 449: 23 p.

Ennis, G.L. 1975. Distribution and abundance of benthic algae along phosphate gradients in Kootenay Lake, British Columbia. Int. Ver. Theor. Angew. Limnol. Verh. 19: 562–570.

Evans, D., and J.G. Stockner. 1972. Attached algae on artificial and natural substrates in Lake Winnipeg, Manitoba. J. Fish. Res. Board Can. 29: 31–44.

Fairchild, G.W., and J.W. Sherman. 1990. Effects of liming on nutrient limitation of epilithic algae in an acid lake. Water Air Soil Pollut. 52: 133–147.

Fairchild, G.W., and J.W. Sherman. 1992. Linkage between epilithic algal growth and water column nutrients in softwater lakes. Can. J. Fish. Aquat. Sci. 49: 1641–1649.

Fairchild, G.W., J.W. Sherman, and F.W. Acker. 1989. Effects of nutrient (N, P, C) enrichment, grazing and depth upon littoral periphyton of a softwater lake. Hydrobiologia 173: 69–83.

Fee, E.J., E.U. Schindler, J.A. Shearer, E.R. DeBruyn, and D.R. DeClerq. 1991. Light attenuation in the mixed-layer of lakes in the Experimental Lakes Area, 1969–1990 data. Can. Data Rep. Fish. Aquat. Sci. 850: 59 p.

Godshalk, G.L., and R.G. Wetzel. 1978. Decomposition of aquatic angiosperms. II. Particulate components. Aquat. Bot. 5: 301–327.

Goldman, J.C., W.J. Oswald, and D. Jenkins. 1974. The kinetics of inorganic carbon limited algal growth. J. Water Pollut. Control Fed. 46: 554–574.

Graham, R.W., and M.A. Turner. 1987. Photoinhibition of respiration in epilithic periphyton. Can. J. Fish. Aquat. Sci. 44(Suppl. 1): 150–153.

Healey, F.P. 1973. Inorganic nutrient uptake and deficiency in algae. Crit. Rev. Microbiol. 3: 69–113.

Healey, F.P. 1979. Short-term responses of nutrient-deficient algae to nutrient addition. J. Phycol. 15: 289–299.

Healey, F.P., and L.L. Hendzel. 1979. Indicators of phosphorus and nitrogen deficiency in five algae in culture. J. Fish. Res. Board Can. 36: 1364–1369.

Hengeveld, H. 1991. Understanding atmospheric change. A survey of the background science and implications of climate change and ozone depletion. State of the Environment Report 91-2. Environment Canada, Ottawa, ON. 68 p.

Howell, E.T., M.A. Turner, R.L. France, M.B. Jackson, and P.M. Stokes. 1990. Comparison of Zygnematacean (Chlorophytal) algae in the metaphyton of two acidic lakes. Can. J. Fish. Aquat. Sci. 47: 1085–1092.

Hutchinson, G.E. 1957. A treatise on limnology. Vol. 1. Geography, physics, and chemistry. John Wiley & Sons, New York, NY. 1015 p.

Jackson, D.F., and B.B. Jackson. 1972. Removal of phosphates in wastewater by the periphyton communities of rotating discs. Int. Ver. Theor. Angew. Limnol. Verh. 18: 881–890.

Kling, H.J., D.L. Findlay, and J.Komárek. 1994. *Aphanizomenon schindleri* sp.nov.: a new nostocacean cyanoprokaryote from the Experimental Lakes Area, northwestern Ontario. Can. J. Fish. Aquat. Sci. 51: 2267–2273.

Loeb, S.L., and J.E. Reuter. 1981. The epilithic periphyton community:

a five-lake comparative study of community productivity, nitrogen metabolism and depth-distribution of standing crop. Int. Ver. Theor. Angew. Limnol. Verh. 21: 346–352.

McCULLOUGH, G.K., AND P. CAMPBELL. 1993. Lake variation and climate change study: ELA lakes, 1986–1990. II. Watershed geography and lake morphology. Can. Tech. Rep. Fish. Aquat. Sci. 1898: 29 p.

MULHOLLAND, P.J., J.W. ELWOOD, A.V. PALUMBO, AND R.J. STEVENSON. 1986. Effect of stream acidification on periphyton composition, chlorophyll, and productivity. Can. J. Fish. Aquat. Sci. 43: 1846–1858.

O'BRIEN, W.J. 1972. Limiting factors in phytoplankton algae: their meaning and measurement. Science (Wash., DC) 178: 616–617.

PARENT, L., M. ALLARD, D. PLANAS, AND G. MOREAU. 1986. The effects of short-term and continuous experimental acidification on biomass and productivity of running water periphytic algae, p. 28–41. *In* B.G. Isom, S.D. Dennis, and J.M. Bates [ed.] Impact of acid rain and deposition on aquatic biological systems. ASTM Spec. Tech. Publ. 928, American Society for Testing and Materials, Philadephia, PA.

PERSSON, G., S.K. HOLMGREN, M. JANSSON, A. LUNDGREN, B. NYMAN, D. SOLANDER, AND C. ANELL. 1977. Phosphorus and nitrogen and the regulation of lake ecosystems: experimental approaches in subarctic Sweden, p. 1–20. *In* Proceedings from Circumpolar Conference on Northern Ecology, Sept. 15–19, 1975, Sect. 2. National Research Council of Canada, Ottawa, ON.

PLANAS, D., L. LAPIERRE, G. MOREAU, AND M. ALLARD. 1989. Structural organization and species composition of a lotic periphyton community in response to experimental acidification. Can. J. Fish. Aquat. Sci. 46: 827–835.

REDFIELD, A.C. 1958. The biological control of chemical factors in the environment. Am. Sci. 46: 204–223.

REUTER, J.E., S.L. LOEB, AND C.R. GOLDMAN. 1983. Nitrogen fixation in periphyton of oligotrophic Lake Tahoe, p. 101–109. *In* R.G. Wetzel [ed.] Periphyton of freshwater ecosystems. Dr. W. Junk, The Hague, The Netherlands.

REUTER, J.E., S.L. LOEB, AND C.R. GOLDMAN. 1986. Inorganic nitrogen uptake by epilithic periphyton in a N-deficient lake. Limnol. Oceanogr. 31: 149–160.

RUDD, J.W.M., C.A. KELLY, D.W. SCHINDLER, AND M.A. TURNER. 1988. Disruption of the nitrogen cycle in acidified lakes. Science (Wash., DC) 240: 1515–1517.

RUDD, J.W.M., C.A. KELLY, D.W. SCHINDLER, AND M.A. TURNER. 1990. A comparison of the acidification efficiencies of nitric and sulfuric acids by two whole-lake addition experiments. Limnol. Oceanogr. 35: 663–679.

SCHINDLER, D.W. 1974. Eutrophication and recovery in experimental lakes: implications for lake management. Science (Wash., DC) 184: 897–899.

SCHINDLER, D.W. 1975. Factors affecting gas exchange in natural waters. Limnol. Oceanogr. 20: 1053–1055.

SCHINDLER, D.W. 1977. Evolution of phosphorus limitation in lakes. Science (Wash., DC) 195: 260–262.

SCHINDLER, D.W., H. KLING, R.V. SCHMIDT, J. PROKOPOWICH, V.E. FROST, R.A. REID, AND M. CAPEL. 1973. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

SHEARER, J.A. 1978. Two devices for obtaining water samples integrated over depth. Can. Fish. Mar. Serv. Tech. Rep. 772: 9 p.

SHEARER, J.A., AND E.R. DEBRUYN. 1986. Phytoplankton productivity responses to direct addition of sulfuric and nitric acids to the waters of a double-basin lake. Water Air Soil Pollut. 30: 695–702.

SHEARER, J.A., E.R. DEBRUYN, D.R. DECLERCQ, D.W. SCHINDLER, AND E.J. FEE. 1985. Manual of phytoplankton primary production methodology. Can. Tech. Rep. Fish. Aquat. Sci. 1341: 58 p.

SHEARER, J.A., E.J. FEE, E.R. DEBRUYN, AND D.R. DECLERCQ. 1987. Phytoplankton primary production and light attenuation responses to the experimental acidification of a small Canadian Shield lake. Can. J. Fish. Aquat. Sci. 44(Suppl. 1): 83–90.

SHELDON, R.B., AND C.W. BOYLEN. 1975. Factors affecting the contribution by epiphytic algae to the primary productivity of an oligotrophic freshwater lake. Appl. Microbiol. 30: 657–667.

SHORTREED, K.S., A.C. COSTELLA, AND J.G. STOCKNER. 1984. Periphyton biomass and species composition in 21 British Columbia lakes: seasonal abundance and response to whole-lake nutrient additions. Can. J. Bot. 62: 1022–1031.

SMITH, E.L. 1936. Photosynthesis in relation to light and carbon dioxide. Proc. Nat. Acad. Sci. U.S.A. 22: 504–511.

STAINTON, M.P., M.J. CAPEL, AND F.A.J. ARMSTRONG. 1977. The chemical analysis of fresh water. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25: 180 p.

STEVENSON, R.J., AND R. GLOVER. 1993. Effects of algal density and current on ion transport through periphyton communities. Limnol. Oceanogr. 38: 1276–1281.

STEVENSON, R.J., C.G. PETERSON, D.B. KIRSCHTEL, C.C. KING, AND N.C. TUCHMAN. 1991. Density-dependent growth, ecological strategies, and effects of nutrients and shading on benthic diatom succession in streams. J. Phycol. 27: 59–69.

STOCKNER, J.G., AND F.A.J. ARMSTRONG. 1971. Periphyton of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. 28: 215–229.

TRAAEN, T.S. 1978. Effects of effluents from a variety of sewage treatment methods on primary productivity, respiration and algal communities in artificial stream channels. Int. Ver. Theor. Angew. Limnol. Verh. 20: 1767–1771.

TURNER, M.A. 1981. Haptobenthic photosynthesis. MSc. thesis, University of Manitoba, Winnipeg, MB. 116 p.

TURNER, M.A., E.T. HOWELL, G.G.C. ROBINSON, J.F. BREWSTER, L.J. SIGURDSON, AND D.L. FINDLAY. 1995a. Growth characteristics of bloom-forming filamentous green algae in the littoral zone of an experimentally acidified lake. Can. J. Fish. Aquat. Sci. 52. (In press)

TURNER, M.A., E.T. HOWELL, M. SUMMERBY, R.H. HESSLEIN, D.L. FINDLAY, AND M.B. JACKSON. 1991. Changes in epilithon and epiphyton associated with experimental acidification of a lake to pH 5. Limnol. Oceanogr. 36: 1390–1405.

TURNER, M.A., M.B. JACKSON, D.L. FINDLAY, R.W. GRAHAM, E.R. DEBRUYN, AND E.M. VANDERMEER. 1987. Early responses of periphyton to experimental lake acidification. Can. J. Fish. Aquat. Sci. 44(Suppl. 1): 135–149.

TURNER, M.A., G.G.C. ROBINSON, B.E. TOWNSEND, B.J. HANN, AND J.A. AMARAL. 1995b. Ecological effects of blooms of filamentous green algae in the littoral zone of an acid lake. Can. J. Fish. Aquat. Sci. 52. (In press)

TURNER, M.A., D.W. SCHINDLER, D.L. FINDLAY, M.B. JACKSON, AND G.G.C. ROBINSON. 1995c. Disruption of littoral algal communities caused by experimental lake acidification. Can. J. Fish. Aquat. Sci. 52. (In press)

TURNER, M.A., D.W. SCHINDLER, AND R.W. GRAHAM. 1983. Photosynthesis–irradiance relationships of epilithic algae measured in the laboratory and *in situ*, p. 73–87. *In* R.G. Wetzel [ed.] Periphyton of freshwater ecosystems. Dr. W. Junk, The Hague, The Netherlands.

WETZEL, R.G. 1964. A comparative study of the primary productivity of higher aquatic plants, periphyton, and phytoplankton in a large, shallow lake. Int. Rev. Gesamten Hydrobiol. 49: 1–61.

WHITFORD, L.A., AND G.J. SCHUMACHER. 1961. Effect of current on mineral uptake and respiration by a fresh-water alga. Limnol. Oceanogr. 6: 423–425.

WHITFORD, L.A., AND G.J. SCHUMACHER. 1964. Effect of a current on respiration and mineral uptake in *Spirogyra* and *Oedogonium*. Ecology 45: 168–170.

Biomanipulation of Lake 221 in the Experimental Lakes Area (ELA): Effects on Phytoplankton and Nutrients[1]

D.L. Findlay, S.E.M. Kasian, L.L. Hendzel, G.W. Regehr, E.U. Schindler, and J.A. Shearer

Department of Fisheries and Oceans, Central and Arctic Region, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada

Findlay, D.L., S.E.M. Kasian, L.L.Hendzel, G.W. Regehr, E.U. Schindler, and J.A. Shearer. 1994. Biomanipulation of Lake 221 in the Experimental Lakes Area (ELA): effects on phytoplankton and nutrients. Can. J. Fish. Aquat. Sci. 51: 2794–2807.

Lake 221 was dominated by omnivorous perch (*Perca flavescens*); the addition of northern pike (*Esox lucius*) resulted in trophic changes that eventually affected the phytoplankton community. Two years following the introduction of pike, perch were greatly reduced. Subsequently, *Chaoborus* abundance increased, rotifer and cladoceran abundance and biomass decreased, and the large-bodied cladoceran *Daphnia catawba* increased. The phytoplankton community shifted from chlorophyte to cyanophyte codominance with dinoflagellates. Phytoplankton biomass and phosphorus (P) increased because of nutrient recycling and excretion by pike and zooplankton. In years three and four, algal biomass and the ratio of suspended to dissolved P decreased because a larger portion of dissolved P was bound in an increased bacterial population. Phytoplankton cell size and production decreased, but the production:biomass ratio increased. In year five, chrysophytes dominated as phytoplankton biomass and production increased and bacterial abundance declined. Phytoplankton responses were primarily an indirect result of the introduction of piscivorous fish, which altered internal nutrient recycling.

La perchaude (*Perca flavescens*), un poisson omnivore, était l'espèce dominante dans le lac 221; l'introduction de grands brochets (*Esox lucius*) a entraîné des changements trophiques qui ont eu un impact sur la communauté phytoplanctonique. Deux ans après l'introduction de grands brochets, la population de perchaude avait grandement décliné. Par la suite, l'abondance de *Chaoborus* a augmenté, les abondances et les biomasses globales de rotifères et de cladocères ont diminué, et la population de *Daphnia catawba*, un cladocère de grande taille, s'est accrue. La dominance des chlorophytes dans la communauté phytoplanctonique a été remplacée par une codominance des cyanophytes et des dinoflagellés. La biomasse de phytoplancton et la quantité de phosphore (P) se sont accrues en raison du recyclage et de l'excrétion des éléments nutritifs par le brochet et le zooplancton. Dans les troisième et quatrième années, la biomasse des algues et la proportion de P en suspension par rapport au P dissous avait chuté parce qu'une plus forte proportion de P dissous se trouvait fixée par les bactéries, dont la population s'était accrue. La production et la taille des cellules du phytoplancton avaient chuté, mais le ratio production:biomasse s'était accrue. Dans la cinquième année, les chrysophycophytes dominaient la communauté phytoplanctonique tandis que la biomasse et la production de phytoplancton s'étaient accrues et que l'abondance des bactéries avait diminué. Les modifications survenues dans la communauté phytoplanctonique étaient essentiellement une conséquence indirecte de l'introduction de poissons piscivores, qui ont altéré les processus internes de recyclage des éléments nutritifs.

Received May 14, 1993
Accepted July 12, 1994
(J11931)

Reçu le 14 mai 1993
Accepté le 12 juillet 1994

In recent years, trophic interactions in aquatic food webs have received a great deal of attention. There are several hypotheses as to how these interactions are regulated. "Biomanipulation" (Shapiro et al. 1975; Shapiro 1980), "trophic cascade" (Carpenter et al. 1985), and "bottom-up – top-down (BUTD)" (McQueen and Post 1985; McQueen et al. 1989) theories hypothesize that top predatory piscivores control the food web in such a way that when abundances of piscivores are high, abundances of phytoplankton are low. These theories acknowledge that nutrient loading is of primary importance in determining maximum algal biomass and production, but they argue that food-chain structure causes variation from the expected trends. There are numerous hypothesized mechanisms that can account for this variation. Knoechel and Holtby (1986), Lynch and Shapiro (1981), and Vanni (1987) documented that zooplankton grazing rates increased exponentially with body size; hence, when large zooplankton are removed by fish, zooplankton grazing rates decreased, allowing phytoplankton to increase. Carpenter and Kitchell (1984) suggested that small zooplankton excrete higher concentrations of specific nutrients than large species, and may be capable of recycling nutrients to the phytoplankton at a greater rate. Elser et al. (1988) demonstrated that zooplankton are important modifiers of nutrient cycling mechanisms. Kitchell et al. (1975) and Nakashima and Leggett (1980) suggested that nutrient inputs via fish excretion are insignificant. Others argued that fish excretion and egestion are significant sources of nutrients (Lamarra 1975; Braband et al. 1985; Reinertsen

[1]This paper is one of a series done in honour of the 25th anniversary of the Experimental Lakes Area.

et al. 1986; Schindler 1992), while Threlkeld (1987, 1988) suggested that dead and decomposing fish are an important nutrient input. Vanni and Findlay (1990) demonstrated in a mesocosm experiment that the mechanism underlying the trophic cascade is that of predators affecting phytoplankton by altering nutrient recycling and zooplankton grazing rate.

A long-term, whole-lake biomanipulation experiment was initiated at the Experimental Lakes Area (ELA) in Lake 221, a small lake with a substantial yellow perch (*Perca flavescens*) population that was primarily zooplanktivorous, although piscivory among the largest size class was probable. The zooplankton community consisted of small rotifers and intermediate-sized *Daphnia galeata mendotae* Birge and *Holopedium gibberum* Zaddach. Two reference years of monitoring (1985 and 1986) preceded the introduction of northern pike (*Esox lucius*) in 1987. Monitoring continued for the following 5 yr (1987–1991). It was hypothesized that the addition of a piscivore would initiate a trophic cascade causing a decrease in the abundance of planktivorous fish, a shift to large-bodied zooplankton, increased grazing pressure by zooplankton on phytoplankton, and reduced phytoplankton biomass and productivity.

The study was designed to investigate changes in species composition and abundance in the major trophic levels. This paper examines the responses of the Lake 221 phytoplankton community and the role of major nutrients over the 7-yr period of observation in relation to trophic interaction theories. The examination of nutrient data and algal physiology data may help in elucidating the essential mechanisms in the trophic cascade.

Methods

Study Site

Lake 221 is a second-order, oligotrophic, brown-water lake situated in the Experimental Lakes Area (ELA), northwestern Ontario (49°38′40″N, 93°43′45″W). It is weakly stratified and dimictic with a surface area of 9 ha and a maximum depth of 5.7 m. A single, intermittent stream flows into the extreme northwestern bay while the lake outflow, controlled by beaver, is located in the northeastern corner. The basin is encompassed by steep hills on the east and west sides. The surrounding watershed is pristine, unlogged boreal forest of jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*).

Within ELA, there is no adequate reference system for Lake 221 based on area, depth, the presence of yellow perch, and the lack of a population of piscivorous fish. Reference Lake 239 was used for comparison to allow separation of biomanipulation effects from climate effects. Findlay and Kasian (1990, 1991) documented that the phytoplankton community in Lake 239 is representative of a suite of ELA reference lakes (109, 224, 373, 382). Oligotrophic Lake 239 is dimictic with a surface area of 56.1 ha and a maximum depth of 30 m. It has a diverse fish population containing piscivores and planktivores, including yellow perch. The Lake 239 watershed was partly burned in 1974 and extensively burned in 1980. Biological, chemical, and physical parameters have been monitored since 1985 on Lake 221 and since 1969 on Lake 239.

Lake 221 in its natural state (1985–86) lacked northern pike or other piscivorous fish, but it supported a predominantly zooplanktivorous fish population of yellow perch and pearl dace (*Margariscus margarita*). The zooplankton assemblage was dominated by small- to intermediate-sized species. The dominant cladocerans were *Daphnia galeata mendotae* and *Holopedium gibberum*. In the spring of 1987, 123 northern pike ranging from 400 to 500 g were removed from ELA Lake 222 and released in Lake 221. This stocking density was considered moderate for ELA lakes (K. Mills, Department of Fisheries and Oceans, Winnipeg, MB, personal communication)

Phytoplankton Sampling and Primary Productivity

In Lakes 221 and 239, water samples were taken using an integrating sampler (Shearer 1978) at intervals from 2 to 4 wk, from a single station located at the position of maximum depth. Samples were taken within the epilimnion and the metalimnion to the depth at which 0.5% surface light occurred. During 1990–1991, samples were taken to the maximum depth at which 1% surface light occurred. Water samples were returned to the laboratory and subsampled for determinations of both phytoplankton populations and photosynthetic carbon (C) uptake.

Ten-millilitre aliquots of the Lugol's preserved samples were gravity settled for 24 h. Phytoplankton species were identified and enumerated using an inverted microscope applying the Ütermohl technique (Nauwerck 1963). Cell counts for each species were converted to wet weight biomass by measuring individual cells of each species, applying the geometric formula best fitted to the cell shape (Vollenweider 1968), and assuming a specific gravity of 1 for cellular mass. Cell sizes were regularly measured and averages were calculated for up to 50 individuals of each species. Based on maximum cell dimension in any direction, species were separated in three size categories: nanoplankton, cells <10 μm; microplankton, cells 10–30 μm; and cells >30 μm.

In 1985, primary production was measured using a ^{14}C radiotracer method as described by Shearer et al. (1985). In 1986, the method was altered slightly (Fee et al. 1992): a single aliquot of inorganic ^{14}C was added to a 1-L subsample, mixed, and siphoned into incubation bottles (cf. earlier years when each bottle was individually spiked with ^{14}C). This change reduced the variance among replicate subsamples but did not result in significantly different production rates. Fee (1990) describes the method applied to calculate integral production.

Bacteria Enumeration

Enumeration of bacteria was not part of the initial experimental design. In 1992, during examination of the changes in dissolved phosphorus (P) and the ratio of primary production to phytoplankton biomass, the existence of an unidentified pool of P became evident and it was hypothesized that the P was bound in bacteria.

Unprocessed water samples for July 1985–1991 were retrieved from the Freshwater Institute's analytical chemistry archives for Lakes 221 and 239. Samples had been stored at 4°C in a dark refrigerator. Selection of samples was based on the timing of annual maximum primary production and water temperature, which generally occurred in July. Prior to archiving, samples had been analyzed for nutrients and weighed, so before subsamples were removed for bacterial enumeration, each sample bottle was reweighed to check for evaporation. Three-millilitre aliquots of unfiltered water samples were removed for bacterial enumeration, which was

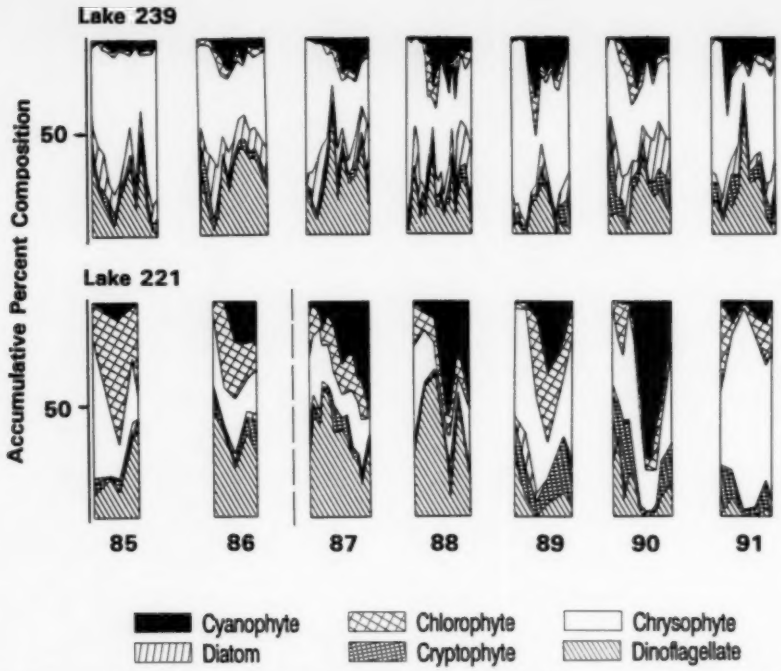


FIG. 1. Cumulative percent composition of phytoplankton by major taxonomic groups for biomanipulated Lake 221 and reference Lake 239 from 1985 to 1991. Vertical broken line indicates introduction of northern pike into Lake 221. All data are euphotic zone values for the open-water season.

performed using epifluorescence microscopy using a Zeiss standard microscope equipped with a mercury lamp. Nonphotosynthetic bacteria were stained using the DAPI technique (Porter and Feig 1980) with a final stain concentration of 1.0 $\mu g \cdot mL^{-1}$. Twenty-four random fields were examined for each sample. To ensure that bacterial growth was not an artifact of storage, July samples previously counted in 1987 from Lakes 239, 373, and 382 and in 1988 from Lake 239 were recounted. The mean difference between the four counts performed in 1987–88 and those recounted in 1992 was 0.39×10^8 cells$\cdot L^{-1}$ or a range from −15 to 34%. There was no obvious trend in these differences from lake to lake.

Chemical Sampling and Methods

Water chemistry samples from the euphotic zones of Lakes 221 and 239 were taken once or twice a month from the same stations as the phytoplankton samples and were analyzed according to Stainton et al. (1977). Discrete samples from 1-, 3-, and 5-m depths in Lake 221 and from 1-, 3-, 5-, and 10-m depths in Lake 239 were obtained using a peristaltic pump. Dissolved and suspended fractions of P, N, and C were measured and total phosphorus (TP), total nitrogen (TN), and total carbon (TC) were calculated. Chlorophyll *a* was measured fluorometrically using a methanol extraction method.

Data Manipulations

The data presented are calculated euphotic zone values. To accommodate the periods of stratification, the individual values for each layer were volume weighted and an euphotic zone estimate was calculated. In Lake 221, the euphotic zone encompassed the entire lake and in Lake 239 it encompassed about the top 10 m.

The BACI (Before:After – Control:Impact) design proposed by Stewart-Oaten et al. (1986, 1992) was used to test whether the biomanipulation resulted in statistically significant changes in biomass of the individual phytoplankton groups. The BACI design uses the difference between a control site (C = Lake 239) and an impacted site (I = Lake 221) as the parameter of interest, and uses samples taken repeatedly through time as replicates. The mean difference of the before period (B = 1986–1987) is compared to the mean difference of the after period (A = 1988–1991). Stewart-Oaten et al. (1986) demonstrated that, as long as other assumptions of the BACI design were met, "pseudoreplication" in time was not a concern. One criterion of BACI is that samples have to be taken at the same time at control and impacted sites. Although the sampling times for Lakes 239 and 221 were frequently up to 1 wk apart, the interval was considered to be short relative to the rate of change of phytoplankton communities. Statistical tests were conducted on before sampling dates to ensure that the assumptions of additivity and independence were met. Data were transformed by log(biomass + 1) before differences were computed to achieve a reasonable level of independence between the differences (C − I) and average amounts of biomass ((C + I)/2). The additivity assumption requiring a constant before difference was tested using linear regression (slope not significantly different from zero) and the Durbin–Watson test (Durbin and Watson 1951) was used to test the independence assumption of no serial correlation. The 1985 and

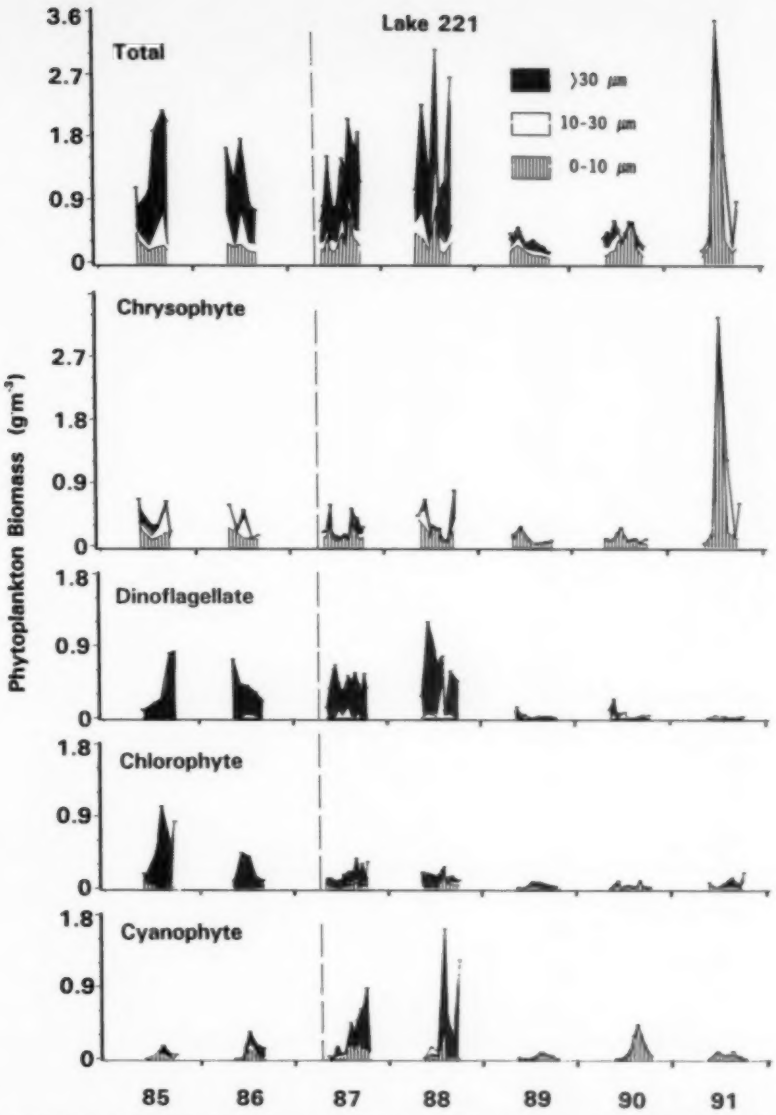


FIG. 2. Daily total phytoplankton biomass and biomass of the major contributing groups for Lake 221, 1985–91, showing the distribution of phytoplankton among three size fractions. The upper line in each panel is equal to the cumulative biomass for that group. The vertical broken line indicates introduction of northern pike. All data are euphotic zone values for the open-water season.

1986 data satisfied both these assumptions ($\alpha = 0.05$). A standard *t*-test (or Satterthwaite's modification for unequal variances) was used to test for a significant change in before and after differences. All statistical tests were done using SAS (SAS Institute Inc. 1990).

Average linkage clustering and principal component analysis (SAS Institute Inc. 1990) were used to examine compositional changes in the phytoplankton community of Lake 221 and to illustrate the similarity of the communities in Lake 239 with two other reference lakes (224 and 373). The correlation matrix of mean annual ice-free biomasses in the euphotic zone (1985–91) of each of seven major phytoplankton groups (cyanophytes, chlorophytes, euglenophytes, chrysophytes, diatoms, cryptophytes, and dinoflagellates) was analyzed.

Results

Phytoplankton Composition, Biomass, and Production

Prior to the biomanipulation (1985–86), chlorophytes (*Botryococcus braunii* Kutz.) and dinoflagellates (*Gymnodinium* sp. and *Peridinium inconspicuum* Lemm.) dominated the phytoplankton community in Lake 221. In contrast, Lake 239 was dominated by chrysophytes (Fig. 1), as are many other

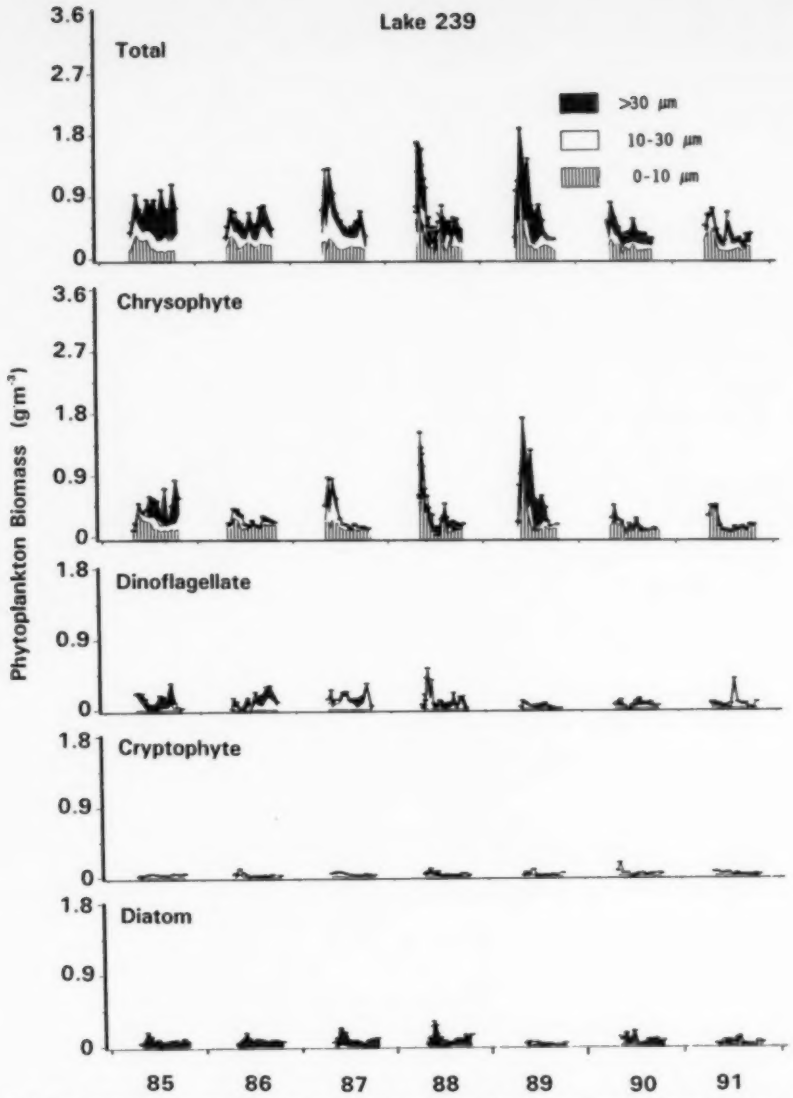


FIG. 3. Daily total phytoplankton biomass and biomass of the major contributing groups for Lake 239, 1985–91, showing the distribution of phytoplankton among three size fractions. The upper line in each panel is equal to the cumulative biomass for that group. All data are euphotic zone values for the open-water season.

unmanipulated ELA lakes. Total phytoplankton biomass ($g \cdot m^{-3}$) in Lake 221 was two times higher than in Lake 239 (Fig. 2 and 3). The nanoplankton and microplankton <30 μm in both lakes were similar, both in species composition and biomass, but algal species >30 μm were considerably more abundant in Lake 221, accounting for the two times difference in biomass (Fig. 2 and 3). Premanipulation, average daily primary productivity (mg $C \cdot m^{-3}$) for the euphotic zone in Lake 221 was two to three times higher than productivity in Lake 239, with average monthly differences in productivity between Lakes 221 and 239 as great as five times in August (Fig. 4a).

In May 1987, 123 northern pike were introduced into Lake 221. Of these, ~111 (K. Mills, personal communication) survived to the fall of 1988 (2 yr after the addition). By 1991, ~74 northern pike existed, but 40% of that estimated population originated from reproduction within Lake 221. Yellow perch were cropped down by northern pike over the first 2 yr (1987–88); the largest individuals disappeared first. In 1991, yellow perch numbers increased (K. Mills, personal communication).

Changes in the zooplankton occurred 2 yr after the fish addition (M. Vanni, Miami University, Oxford, Ohio, personal communication). The rotifer population dramatically declined in 1989 and 1990, as did the abundance of *Daphnia galeata mendotae*. As hypothesised by M. Vanni (personal communication), a large cladoceran appeared in 1988 (*Daphnia catawba*) and increased thereafter. The Lake 221 *Chaoborus*

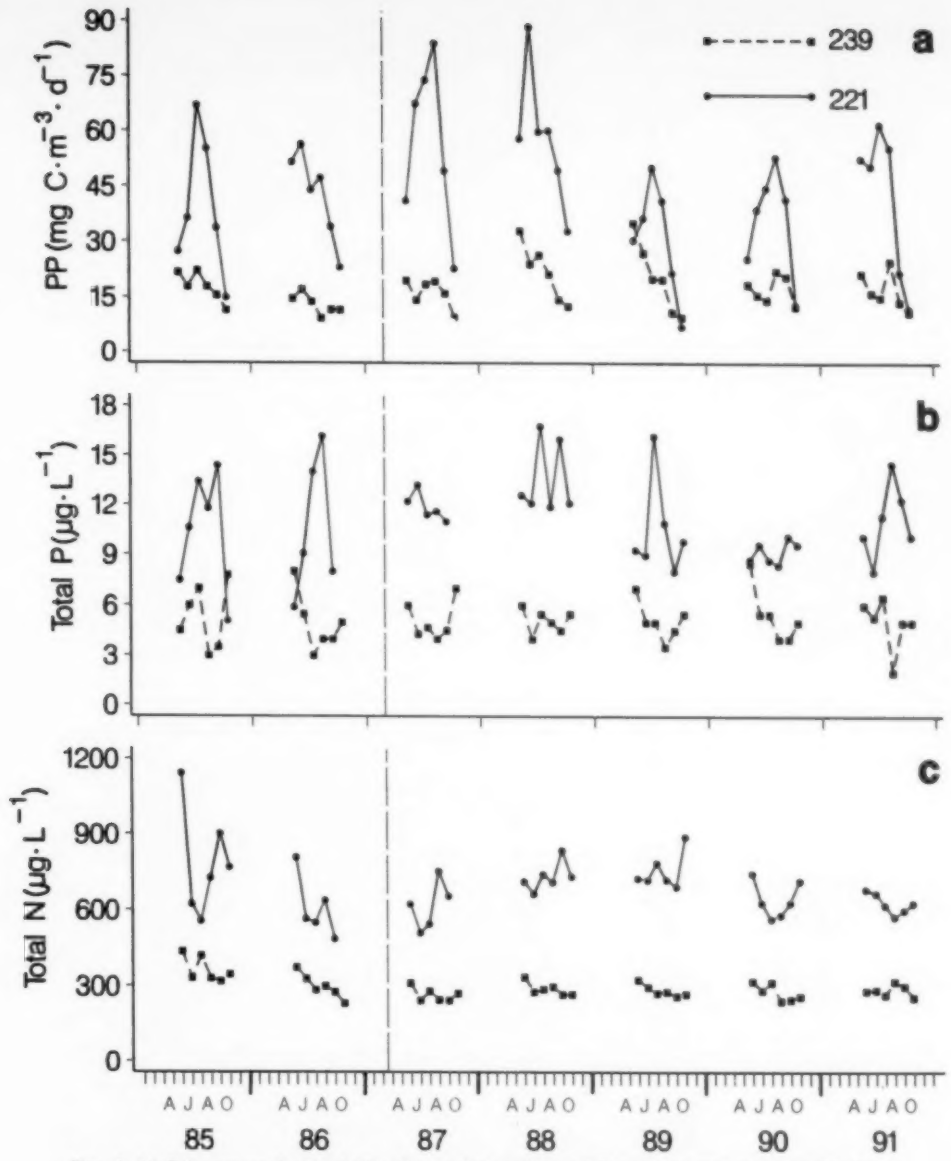


FIG. 4. (a) Primary production (PP), (b) total phosphorus (P), and (c) total nitrogen (N) in the euphotic zone on each sampling day through the open-water season for Lakes 221 and 239, 1985–91. Vertical broken line indicates introduction of northern pike into Lake 221.

population was monitored infrequently over the 7 yr of the study; samples were taken in 1985–87 and 1990. Over this time the species shifted from the small *Chaoborus punctipennis* (in the early years) to the large *Chaoborus flavicans* (in 1990).

In 1987, total phytoplankton biomass in Lake 221 remained similar to premanipulation estimates. It increased slightly in 1988 (Fig. 2). Average daily primary productivity increased over premanipulation values in both 1987 and 1988 (Fig. 4a). During this period similar trends were observed in Lake 239 (Fig. 3 and 4a). Throughout 1987–88 dinoflagellates continued to dominate the Lake 221 phytoplankton assemblage, but chlorophytes (*Botryococcus braunii*) decreased as coccoidal cyanophytes (*Merismopedia tenuissima* Lemm. and *Rhabdogloea linearis* Komar.) and colonial cyanophytes (*Gomphospaerium lacustris* Chod.) increased (Fig. 1 and 2). These species shifts had little effect on the size structure of the phytoplankton assemblage (Fig. 2).

In 1989–90, total phytoplankton biomass in Lake 221 decreased 80% from 1988 (Fig. 2). A 40% decrease in productivity occurred over the same period (Fig. 4a), so the production/biomass ratio increased (Fig. 5). Species composition was transitory, and no specific group or species dominated during this time (Fig. 1 and 2). Large dinoflagellates and colonial cyanophytes >30 µm virtually disappeared by 1989–90. Chrysophytes were abundant in spring and fall. Small chlorophytes dominated in the summer of

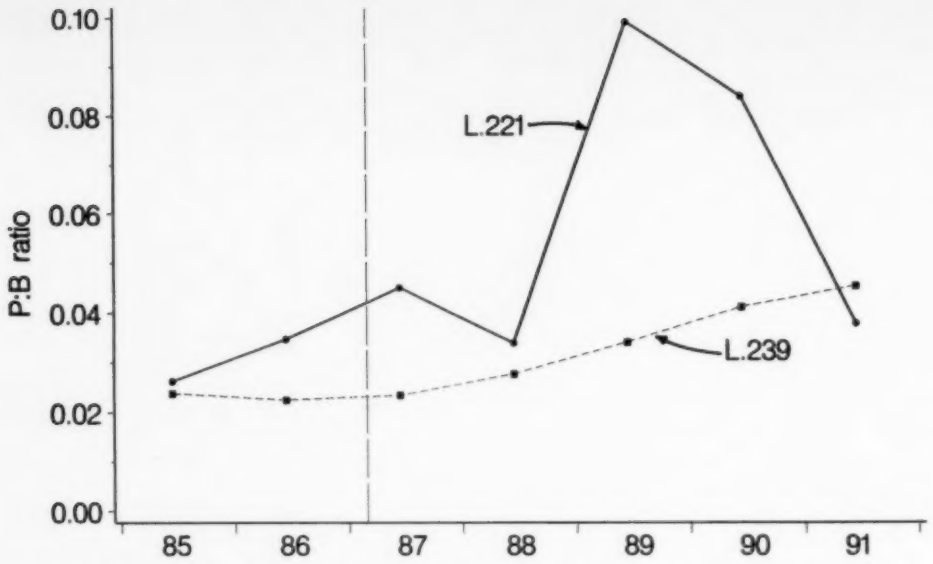


FIG. 5. Ratio of mean daily primary production (P, mg C·d^{-1}) to phytoplankton biomass (B, mg) for Lakes 221 and 239, 1985–91. Vertical broken line indicates introduction of northern pike into Lake 221.

1989 and coccoidal cyanophytes <10 μm dominated in the summer of 1990 (Fig. 1 and 2). Nanoplankton and microplankton <30 μm biomasses remained as before, but cells >30 μm were greatly reduced. In contrast, the average biomass of Lake 239 phytoplankton resembled previous years during 1989 and 1990 (Fig. 3).

In 1991, total phytoplankton biomass in Lake 221 increased 2.6 times over 1990 estimates, returning to premanipulation levels (Fig. 2). Chrysophytes dominated over the entire season, which was similar to Lake 239 (Fig. 3). Increased summer biomass was associated with chrysophycean blooms of the nanoplankton *Chrysochromulina laurentiana* in July and the microplankton *Dinobyron bavaricum* in August. These blooms occurred after a cool, cloudy, wet period in early July. There was no significant increase in nutrient loading to Lake 221 from precipitation from 1990 to 1991 in July. Average daily primary productivity in Lake 221 also increased slightly during this period (Fig. 4a).

The results of initial t-tests (1985–86 vs. 1987–91) using the BACI design indicated that only chlorophytes showed a significant ($P < 0.05$) change in biomass from before to after manipulation. The power of BACI to detect changes is considerably decreased if the after differences are not constant (Stewart-Oaten et al. 1986). The annual mean ratios plotted in Fig. 6a indicate differences that vary by discrete time periods. One-way ANOVAs, with after years treated separately, were used instead of t-tests on before vs. after to examine the responses in more detail. All taxonomic groups, as well as total biomass, indicated significant differences among years at the probabilities indicated in Fig. 6b. Duncan's Multiple Range test on mean annual differences revealed that only cyanophytes showed an immediate response in 1987 and 1988 (Fig. 6b). For most of the other groups, significant changes did not occur until 1989 or 1990. In 1991, only chrysophytes and dinoflagellates were significantly different from before manipulation values.

Combined responses of the seven major taxonomic groups were assessed using cluster analysis, which separated the 7 yr of data from Lake 221 in three groups. The first 2 yr of the manipulation (1987–88) were clustered with the premanipulation years (1985–86). The years 1989 and 1990 for Lake 221 were grouped with the 19-yr suite of reference lakes (224, 1985–91; 239, 1985-91; 373, 1985–87 and 1990–91). Lake 221, 1991, was grouped alone.

Principal component analysis confirmed these results (Table 1; Fig. 7). Principal component 1 (PC1), which accounted for 41% of the total variance, separated the data in two major groups based on either high abundances of dinoflagellates and cyanophytes or high abundances of chrysophytes. Based on this axis, Lake 221 prior to and during the first 2 yr of manipulation (1985–88) had a distinctly different phytoplankton composition and biomass than Lakes 224, 239, and 373 over the whole period. The PC1 axis also indicated that the composition of the Lake 221 phytoplankton community in 1989 and 1990 had shifted towards that of the reference lakes. The second principal component (PC2) accounted for 21% of the variance and indicated the predominance of cryptophytes, which were a major factor of variance in the reference lakes. The third principal component (PC3) accounted for an additional 19% of the variance, which separated high chlorophycean abundance from high diatom abundance. In 1991, Lake 221 had conspicuously high chrysophycean abundance, similar to the reference lakes, and high abundances of chlorophytes and cryptophytes.

Nutrients and Algal Physiological Status

On average, TP and TN concentrations in Lake 221 were two times those in Lake 239 (Fig. 4b and 4c). From 1985 to 1991, TN remained stable in both Lakes 221 and 239 (Fig. 4c). On average, TP in Lake 221 increased 30% in 1987–88, a trend not evident in Lake 239, but declined in the

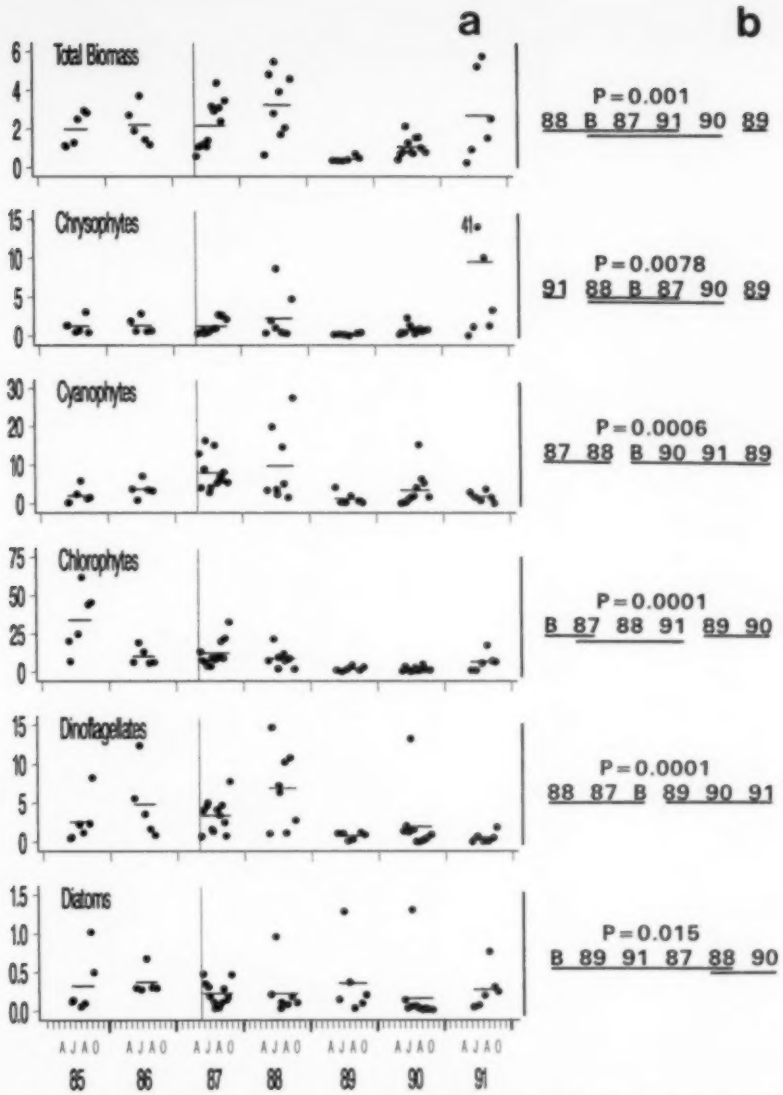


FIG. 6. (a) Ratios of Lake 221 to Lake 239 for total phytoplankton biomass and each major taxonomic group within the euphotic zone. Dots are ratios on each sampling day through the open-water season; horizontal lines are the mean ratio for each year. Ratios are shown instead of differences of log(biomass + 1) to maintain an arithmetic scale and because log(I) − log(C) = log(I/C) (C = control site; I = impacted site). (b) ANOVA probabilities (P) indicating overall significant differences among years. B = mean of 1985–86. Years joined by the same underline are not significantly different. Yearly mean ratios are ranked highest to lowest from left to right.

following years (Fig. 4b). In Lake 221, no consistent seasonal pattern for P was apparent although concentrations were generally higher during July. Total P concentrations in Lake 239 were consistently higher in May than during other times of the year, but varied little over the remainder of the season. The ratio of suspended P to dissolved P in Lake 221 decreased 50% in 1989 and remained low for the following years as a result of decreased suspended P and increased dissolved P (Table 2). In contrast, the ratio in Lake 239 decreased gradually throughout the same period because of increased dissolved P (Table 2).

The 7-yr record of algal nutrient status indicators (Healey 1975) such as suspended C/chlorophyll *a* (Fig. 8a), suspended C/P (Fig. 8b), and suspended N/P (Fig. 8c) ratios were similar in Lakes 221 and 239. However, the phytoplankton community in Lake 239 was generally more severely nutrient deficient than the Lake 221 community (Fig. 8a). The suspended N/P and C/P ratios indicated that both lakes were moderately to severely P deficient (Fig. 8b and 8c). The suspended C/P and N/P ratios for 1989–90 indicated a reduced P deficiency offset by an increased N deficiency in May and June in Lake 221.

TABLE 1. Summary of results from principal component analysis on phytoplankton biomass in each major taxonomic group for Lakes 221 and 239. Shown are the loadings for the first three principal component axes (PC1–PC3) and the percent variances accounted for by each axis.

	% variance	Cyanophyte	Chlorophyte	Chrysophyte	Diatom	Cryptophyte	Dinoflagellate
PC1	41	0.46	0.32	−0.57	−0.37	−0.08	0.46
PC2	21	0.19	0.32	−0.05	−0.20	0.75	−0.51
PC3	19	0.29	−0.52	−0.29	0.56	0.44	0.24

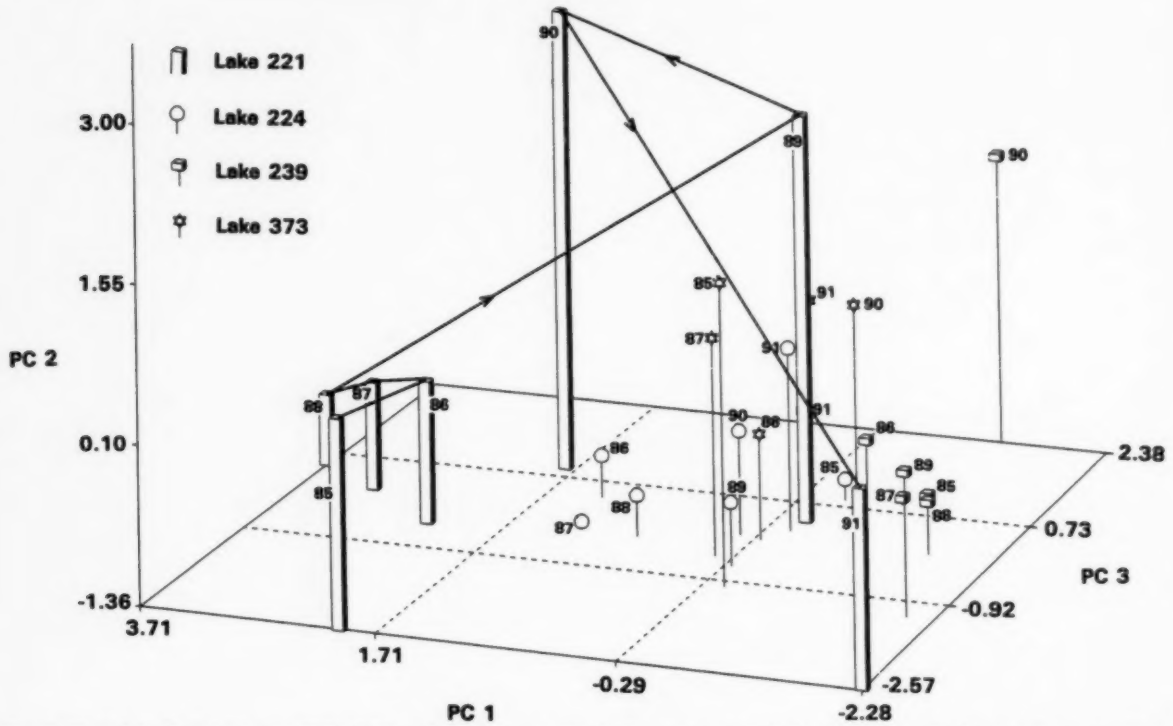


FIG. 7. Plot of the first three axes (PC1, PC2, and PC3) from a principal component analysis of annual euphotic zone, open-water season total biomasses for each of the seven major taxonomic groups for reference Lakes 224, 239, and 373 and for Lake 221.

Bacteria

Pelagic bacteria in Lake 221 increased in abundance three times over premanipulation estimates in 1989 and 1990 and decreased in 1991 (Fig. 9). Bacterial abundance in Lake 239 for 1985–91 was relatively stable, averaging $3.67 \times 10^8 \pm 0.79 \times 10^8$ cells·L^{-1}. Bacterial abundances recorded for Lakes 221 and 239 are comparable with literature estimates for other oligotrophic lakes (Hobbie et al. 1977; Pomroy 1984; Nishino 1986). Bacterial abundance and phytoplankton biomass were inversely correlated in Lake 221 (r^2 = 0.95, P = 0.001), but no such relationship existed in Lake 239 (r^2 = 0.01, P = 0.87).

Assuming a maximum cell diameter of 1 μm (the bacteria passed through a 1-μm filter) and a density of 1 results in a biomass estimate of 0.52 pg·cell^{-1}. Therefore, Lake 239 had an estimated bacterial biomass ranging from 0.13 to 0.22 g·m^{-3}. Lake 221 prior to manipulation had a bacterial biomass of 0.13 g·m^{-3}, which increased to a maximum in 1990 of 0.46 g·m^{-3}.

Discussion

The introduction of a top predator (northern pike) to Lake 221 directly and indirectly caused major changes in the phytoplankton community that largely support the hypothesis of a "trophic cascade." During the 5 yr of the biomanipulation, community structure of the Lake 221 phytoplankton progressed through three phases, whereas community structure was unchanged in reference Lake 239. Long-term monitoring of algal populations in the ELA has documented that natural phytoplankton community structures are stable (Findlay and Kasian 1990, 1991). The premanipulation phytoplankton composition and biomass in Lake 221 were distinctly different from Lake 239. Throughout each subsequent phase, the phytoplankton community in Lake 221, dominated previously by planktivorous fish, began to resemble that of Lake 239 and other reference lakes containing piscivorous species.

The first phase (1987–88) was a period of community adjustment characterized by a shift in phytoplankton species

TABLE 2. Mean annual suspended phosphorus (P), total dissovled phosphorus (TDP), total phytoplankton biomass, suspended P / TDP, and suspended P / biomass ratio for Lakes 221 and 239 for the open-water season.

Year	Suspended P ($\mu g \cdot L^{-1}$)	TDP ($\mu g \cdot L^{-1}$)	Phytoplankton biomass ($g \cdot m^{-3}$)	Suspended P TDP ($\mu g \cdot \mu g^{-1}$)	Suspended P biomass ($\mu g \cdot mg^{-1}$)
			Lake 221		
1985	7.7	2.8	1.48	2.8	5.2
1986	7.3	3.3	1.23	2.2	5.9
1987	8.2	3.5	1.25	2.4	6.6
1988	9.3	4.2	1.71	2.2	5.4
1989	5.3	5.2	0.29	1.0	18.3
1990	4.9	4.1	0.43	1.2	11.4
1991	6.2	4.5	1.12	1.4	5.5
			Lake 239		
1985	4.3	1.2	0.75	3.5	5.7
1986	3.3	1.4	0.56	2.4	5.9
1987	3.1	2.0	0.70	1.5	4.4
1988	3.5	1.7	0.81	2.0	4.3
1989	3.0	2.1	0.82	1.4	3.7
1990	3.1	2.5	0.44	1.2	7.0
1991	3.3	2.0	0.40	1.7	8.3

composition from premanipulation community structure. This was accompanied by a moderate increase in phytoplankton biomass and P concentration. The hypothesized response was a decrease in algal biomass as observed by Vanni and Findlay (1990) in enclosure experiments in the same lake. The lack of a major response by the phytoplankton community in Lake 221 in the initial years (1987–88) was probably a result of the moderate stocking density of pike relative to perch abundance and to the effects of predation having to filter down through several higher trophic levels. Before the introduction of the northern pike, the perch population had two distinct size classes (K. Mills, personal communication). In the initial year of the biomanipulation, the numbers of large perch decreased and this was followed in 1988 by a reduction in numbers of smaller fish. Therefore, the loss of the larger, probably omnivorous, perch had little or no immediate effect on zooplankton biomass (M. Vanni, personal communication). It was not until the end of the 1988 season that the smaller zooplanktivorous perch were decimated by the northern pike. The moderate increase in phytoplankton biomass in the presence of an unchanged zooplankton biomass can be attributed to elevated P levels.

The increased P (30%) in Lake 221 was probably generated by internal recycling rather than external inputs because annual precipitation was 22% less in 1987–88 than in 1985–86; as a result, annual loading of P directly to the lake surface decreased 29% (M. Stainton and K. Beaty, Department of Fisheries and Oceans, Winnipeg, MB, personal communication). Campbell (1994) examined two small lakes in the ELA (1990–1992) containing piscivores and documented only a 10–15% variation in average total P for the open-water season. The addition of the northern pike to Lake 221 could not be considered a significant input source of P. Assuming P is 0.5% of fresh body weight (Arai et al. 1975; Lall and Bishop 1977; Shearer 1984), 1.5 μg $P \cdot L^{-1}$ of lake water, bound in fish, was added to the lake. Ninety percent of the original fish stock existed in the fall of 1988 and, therefore, significant amounts of P could not have been released through decomposition. Phytoplankton species shifts and increased biomass in the first 2 yr following the fish introduction were most likely a result of alteration in P cycles via fish excretion, and preferential grazing and nutrient recycling by zooplankton. During 1987–88 the northern pike all but eliminated the yellow perch population (K. Mills, personal communication). A portion of the perch biomass was probably excreted by northern pike, accounting for some of the increase in usable P. Nutrient status indicators (Fig. 8) suggest that P remained the limiting nutrient and, therefore, was the major controlling influence on attainable phytoplankton biomass. In situ enclosure experiments in Lake 221, in which abundances of *Daphnia catawba*, *Chaoborus americanus*, and yellow perch were manipulated, showed phytoplankton species shifts and increases in biomass similar to those that occurred in 1987–88 (Vanni and Findlay 1990). Responses in the enclosures were attributed to the fish altering P cycling both directly through their excretion–egestion and indirectly through effects on zooplankton excretion and composition.

The second phase could be described as a clear-water phase, occurring in years 3 and 4 of the manipulation of Lake 221 (1989–90). This phase conformed to the effect predicted by trophic cascade theories. Total phytoplankton biomass, primary productivity, and the >30-μm fraction of phytoplankton decreased significantly (Fig. 2, 3, and 4a). Small, colonial chrysophytes and gelatinous sheathed chlorophytes and cyanophytes constituted the majority of biomass. The concentration of total P in Lake 221 decreased slightly, returning to premanipulation levels, phytoplankton biomass decreased dramatically (80%) and the suspended to dissolved P ratio decreased 50% (Table 2).

There are several possible explanations for the lack of a direct relationship between phytoplankton biomass and

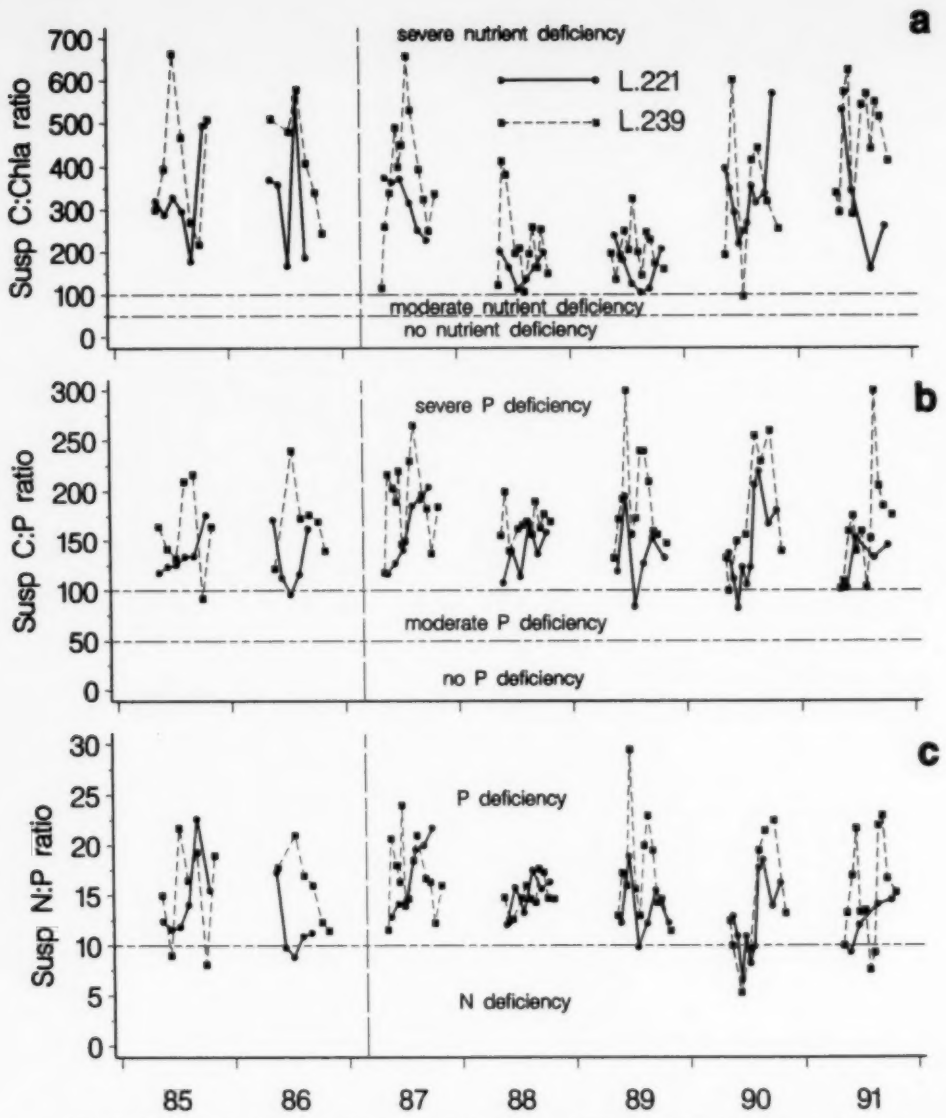


FIG. 8. Algal nutrient status indicators for Lakes 221 and 239, 1985–91, for the euphotic zone during the open-water season. Ratio (by weight) of (a) suspended (C) / chlorophyll *a*, (b) suspended C / suspended phosphorus (P), and (c) suspended nitrogen (N) / suspended P. Vertical broken line indicates introduction of northern pike into Lake 221.

total P. We hypothesize that the effects seen in the phytoplankton community are a combination of direct and indirect pressures exerted by zooplankton and fish. The effects of zooplankton grazing are the most obvious. Increased grazing will transfer P to zooplankton, allowing accumulation of available P as algal biomass becomes limited by grazing. Food web manipulations resulted in a shift in the zooplankton population to larger cladocerans, but these large zooplankton were insufficiently abundant to account for such a dramatic decrease in phytoplankton biomass through grazing pressure (M. Vanni, personal communication). The increased dissolved P / suspended P could be explained by zooplankton grazing and/or excretion, but nutrient status indicators did not demonstrate reduction of P deficiency. Therefore, much of the increased dissolved P was apparently unavailable for algal growth.

Food web alterations can result in changes in zooplankton composition that favour species capable of altering supply rates of major nutrients (e.g., *Daphnia* spp., which can alter the N/P in excreted material) (Elser et al. 1988). Although total dissolved P in Lake 221 increased slightly, there was no obvious change in the seston N/P ratio, indicating that zooplankton did not affect supply rates in our study.

A more plausible explanation for low algal biomass with increased TDP is that P was bound in bacteria. The analytical method used to measure dissolved P requires filtering the

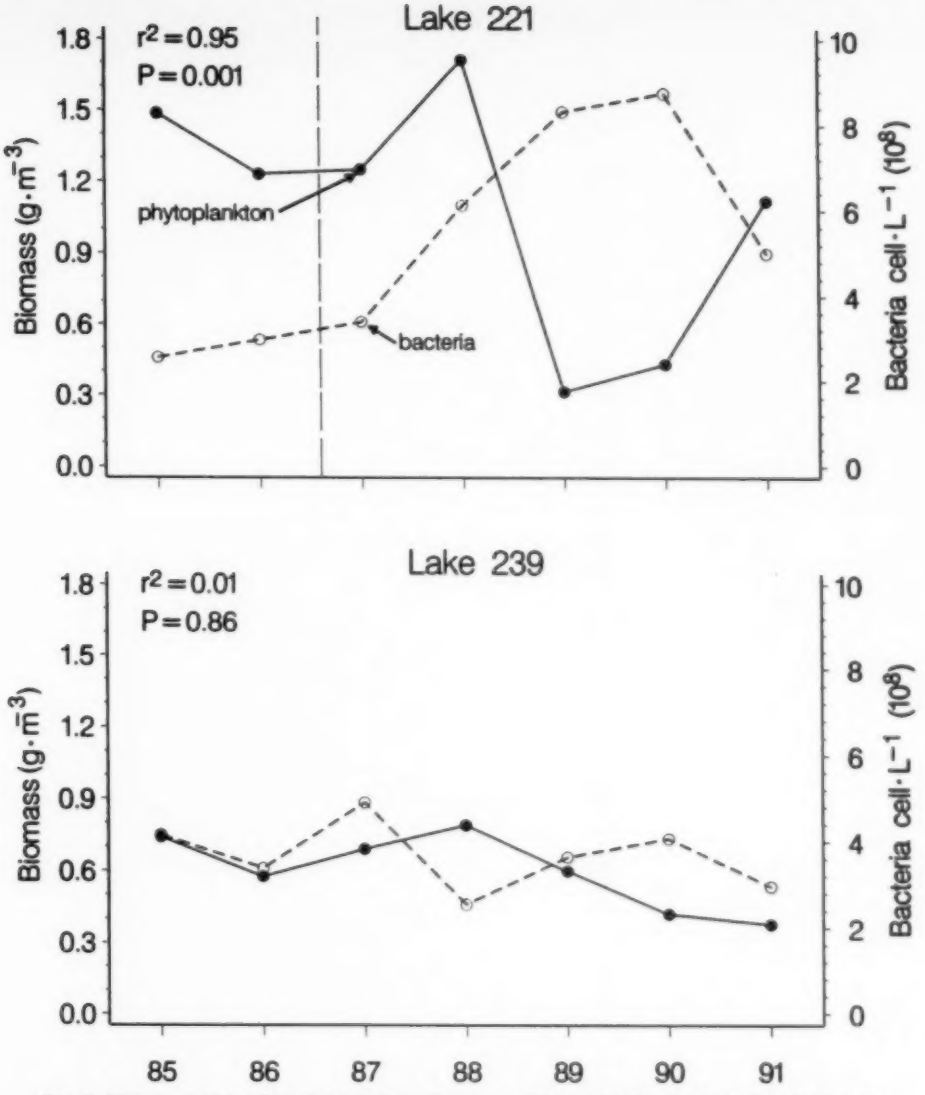


FIG. 9. Mean annual ice-free phytoplankton biomass and bacterial abundance in July for Lakes 221 and 239, 1985–91. Vertical dotted line indicates introduction of northern pike.

sample through a 1-μm filter, which would allow bacteria to be included in the dissolved fraction. Although only mid-summer samples were examined, bacterial abundance increased in Lake 221 during 1989 and 1990 (Fig. 9). In the absence of grazing pressure by zooplankton, it has been shown that bacteria generally outcompete phytoplankton for available P (Carpenter et al. 1992; Rothhaupt 1992). It is conceivable that bacteria could account for sufficient P even though bacterial biomass accounted for only one third of the lost phytoplankton biomass. Vadstein et al. (1988), Tezuka (1990), and Hessen and Andersen (1992) reported that P/C ratios can be as much as five times greater in bacteria than in phytoplankton.

During this phase, production/biomass ratio increased while algal biomass was very low (Fig. 5). In addition, nutrient status indicators suggested that the ability of the algae to utilize nutrients had not markedly improved (Fig. 8). Because maximum growth rates are size dependent (Schlesinger et al. 1981; Nielson and Sand-Jensen 1990), we postulate that the production/biomass ratio increased because of the loss of larger algal species. Smaller species are faster growing than larger species and, therefore, contribute to a higher production/biomass ratio.

M. Vanni (personal communication) reported a decrease in planktivorous perch and rotifers, a shift in cladoceran body size, and an increase in *Chaoborus* abundance in 1989. We hypothesize that the pike added to Lake 221 decreased the abundance of perch, relieving predation pressure on *Chaoborus*. The *Chaoborus* population increased, reducing the rotifer population, and the larger cladocerans grazed down the ciliate and heterotrophic nanoflagellate populations, allowing bacteria to outcompete phytoplankton for P.

Chaoborus prey on rotifers (Swift 1976; Neill 1981); cladocerans are capable of ingesting ciliates and heterotrophic nanoflagellates (McMahon and Rigler 1965; Porter et al. 1979; Archbold and Berger 1985; and Sanders and Porter 1990); and rotifers, ciliates, and heterotrophic nanoflagellates are capable of feeding on bacteria (Fenchel 1980; Jonsson 1986; Sanders et al. 1989; Sanders and Porter 1990).

The third phase began in year five of the Lake 221 manipulation (1991) and was different from other years because of the dominance of chrysophytes. Concurrent with this shift was an increase to premanipulation levels of total phytoplankton biomass (Table 2), nanoplankton and microplankton biomass (Fig. 2), and primary productivity (Fig. 4a). Algal status measurements indicated that P limitation still existed even though annual mean P concentration did not significantly change (Fig. 8). Populations of yellow perch increased during this period as northern pike abundance declined (K. Mills, personal communication). Young-of-the-year perch are voracious feeders on zooplankton and *Chaoborus* (Vanni and Findlay 1990), possibly resulting in decreased grazing pressure on the rotifer and phytoplankton populations. Subsequently, grazing pressure by rotifers on bacteria and nanoplankton would have increased. Climatic conditions in 1991 may have contributed to this phase. The spring was wet and cool and it was followed by a warm, early summer. The beginning of July was cloudy and cool, followed by the driest August and wettest September on record (K. Beaty, unpublished data). The dominant chrysophycean species in 1991, *Dinobryon bavaricum* and *Chrysochromulina laurentiana*, are favoured by cool, low light conditions (O'Grady 1987), which may have allowed them to outcompete *Botryococcus braunii*, the previously dominant chlorophycean species. In addition, *Dinobyon* and *Chrysochromulina* are voracious predators of bacteria (Bird and Kalf 1989), and so the dramatic increase in populations of these chrysophytes in 1991 may be a response to increased bacterial abundances in 1990. Reversing a piscivore addition does not necessarily allow the phytoplankton community to recover quickly (Carpenter et al. 1992). Lake 221 is a second-order lake, so species present prior to the manipulation are available for recolonization. In 1991, the northern pike population was 50% of its original stocked density, and the planktivorous perch had increased in abundance. Compositional shifts in phytoplankton species and fluctuating phytoplankton biomass continue to indicate that the Lake 221 ecosystem is responding as a perturbed system.

Over the course of the last 10–15 yr there have been many whole-lake biomanipulation experiments reported in the literature. These experiments have been done over different lengths of time and have focused on different parts of the food web. The biomanipulation of Lake 221 was unique because the lake originally had no large piscivorous predators, it was studied for a prolonged period before and after manipulation, and plankton community responses were examined at the species level. The cycling of nutrients by processes such as excretion, grazing, and nutrient retention, and the role of bacteria in nutrient cycling require further study.

Acknowledgements

We thank E. Debruyn and D. Cruikshank for collecting the phytoplankton samples. The ELA and Winnipeg analytical chemistry laboratories performed all chemical analyses. R. Schade supplied valuable assistance in obtaining samples from the chemical archives. R. Hecky, R. Hesslein, M. Vanni, H. Welch, M. Paterson, D. Rosenberg, and J. Elser offered constructive criticisms during preparation of this manuscript.

References

Archbold, J.H.G., and J. Berger. 1985. A qualitative assessment of some metazoan predators of *Halteria grandinella*, a common freshwater ciliate. Hydrobiologia. 126: 97–102.

Arai, S., R. Muller, Y. Shimma, and T. Nose. 1975. Effects of calcium supplement to yeast grown on hydrocarbons as a feedstuff for rainbow trout. Bull. Freshwater Fish. Res. Lab. 25: 33–40.

Bird, D.F., and J. Kalff. 1989. Phagotrophic sustenance of a metalimnetic phytoplankton peak. Limnol. Oceanogr. 34: 155–162.

Braband, A., B.A. Faafeng, and J.P. Nilssen. 1985. Fish and nutrient dynamics in a deep, mesotrophic lake. Int. Ver. Theor. Angew. Limnol. Verh. 19: 2553.

Campbell, P. 1994. Phosphorus budgets and stoichiometry during the open-water season in two unmanipulated lakes in the Experimental Lakes Area, northwestern Ontario. Can. J. Fish. Aquat. Sci. 51: 2739–2755.

Carpenter, S.R., K.L. Cottingham, and D.E. Schindler. 1992. Biotic feedbacks in lake phosphorus cycles. TREE 7(10): 332–336.

Carpenter, S.R., and J.F Kitchell. 1984. Plankton community structure and limnetic primary production. Am. Nat. 124: 159–172.

Carpenter, S.R., J.F Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake ecosystem productivity. BioScience 35: 635–639.

Durbin, J. and G.S. Watson. 1951. Testing for serial correlation in least squares regression. Biometrika 37: 409–428.

Elser, J.J., M.M. Elser, N.A. MacKay, and S.R. Carpenter. 1988. Zooplankton-mediated transitions between N and P limited algal growth. Limnol. Oceanogr. 33: 1–14.

Fee, E.J. 1990. Computer programs for calculating *in situ* phytoplankton photosynthesis. Can. Tech. Rep. Fish. Aquat. Sci. 1740: 27 p.

Fee, E.J., J.A. Shearer, E.R. DeBruyn, and E.U. Schindler. 1992. The effect of lake size on phytoplankton photosynthesis. Can. J. Fish. Aquat. Sci. 49: 2445–2459.

Fenchel, T. 1980. Relation between particle size selection and clearance in suspension-feeding ciliates. Limnol. Oceanogr. 25: 733–738.

Findlay, D.L., and S.E.M. Kasian. 1990. Phytoplankton communities of lakes experimentally acidified with sulfuric and nitric acids. Can. J. Fish. Aquat. Sci. 47: 1378–1386.

Findlay, D.L., and S.E.M. Kasian. 1991. Response of a phytoplankton community to controlled partial recovery from experimental acidification. Can. J. Fish. Aquat. Sci. 48: 1022–1029.

Healey, F.P. 1975. Physiological indicators of nutrient deficiency in algae. Can. Fish. Mar. Serv. Tech. Rep. 585: 30 p.

Hessen, O.D., and T. Andersen. 1992. The algae-grazer interface: feedback mechanisms linked to elemental ratios and nutrient cycling. Ergeb. Limnol. 35: 11–120.

Hobbie, J.E., R.J. Daley, and S. Jasper. 1977. Use of Nuclepore filters for counting bacteria by fluorescence microscopy. Appl. Environ. Microbiol. 33: 1225–1228.

Jonsson, P.R. 1986. Particle size, feeding rates and growth dynamics of marine planktonic oligotrichous ciliates (Ciliophora: Oligotrichina). Mar. Ecol. Prog. Ser. 33: 265–277.

Kitchell, J.F., J.F. Koonce, and P.S. Tennis. 1975. Phosphorus flux through fish. Int. Ver. Theor. Angew. Limnol. Verh. 19: 2478–2484.

Knoechel, R., and L.B. Holtby. 1986. Construction and validation of a body-length-based model for the prediction of cladoceran community filtering rates. Limnol. Oceanogr. 31: 1–16.

Lall, S.P. and F.J. Bishop. 1977. Studies on mineral and protein utilization by Atlantic salmon (*Salmo salar*) grown in sea water. Can. Fish. Mar. Serv. Tech. Rep. 688: 16 p.

Lamarra, V.A. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. Int. Ver. Theor. Angew. Limnol. Verh. 19: 2461–2468.

Lynch, M., and J. Shapiro. 1981. Predation, enrichment, and phytoplankton community structure. Limnol. Oceanogr. 26: 92–102.

McMahon, J.W., and F.H. Rigler. 1965. Feeding rates of *Daphnia magna* Straus in different food labelled with radioactive phosphorus. Limnol. Oceanogr. 10: 105–113.

McQueen, D.J., M.R.S. Johannes, J.R. Post, T.J. Stewart, and D.S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. 59: 289–309.

McQueen, D.J., and J.R. Post. 1985. Effects of planktivorous fish on zooplankton, phytoplankton and water chemistry, p 35–42. *In* Lake and Reservoir Management: Practical Applications. Proceedings of the Fourth International Conference and International Symposium, North American Lake Management Society (NALMS), October 1984, McAfee, NJ. American Lake Management Society, Washington, D.C.

Nakashima, B.S., and W.C. Leggett. 1980. The role of fishes in the regulation of phosphorus availability in lakes. Can. J. Fish. Aquat. Sci. 37: 1540–1549.

Nauwerck, A. 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton in See Erken. Symb. Bot. Ups. 17: 163 p.

Neill, W.E. 1981. Impact of *Chaoborus* predation upon the structure and dynamics of a crustacean zooplankton community. Oecologia 48: 164–177.

Nielsen, S.L., and K. Sand-Jensen. 1990. Allometric scaling of maximal photosynthetic growth rate to surface/volume ratio. Limnol. Oceanogr. 35: 177–181.

Nishino, S.F. 1986. Direct acridine orange counting of bacteria preserved with acidified Lugol iodine. Appl. Environ. Microbiol. 52: 602–604.

O'Grady, K.A. 1987. Light, temperature and nitrogen interactions in two freshwater algae from lakes undergoing acidification. Ph.D. thesis, University of Western Ontario, London, ON. 167 p.

Pomroy, A.J. 1984. Direct counting of bacteria preserved with Lugol iodine solution. Appl. Environ. Microbiol. 47: 1191–1192.

Porter, K.G., and Y.S. Feig. 1980. The use of DAPI for identifying and counting aquatic microflora. Limnol. Oceanogr. 25: 943–948.

Porter, K.G., M.L. Pace, and J.F. Battey. 1979. Ciliate protozoans as links in freshwater planktonic food chains. Nature (Lond.) 277: 563–565.

Reinertsen, H., A. Jensen, A. Langeland, and Y. Olsen. 1986. Algal competition for phosphorus: the influence of zooplankton and fish. Can. J. Fish. Aquat. Sci. 43: 1135–1141.

Rothhaupt, K.O. 1992. Stimulation of phosphorus-limited phytoplankton by bacterivorous flagellates in laboratory experiments. Limnol. Oceanogr. 37: 750–759.

Sanders, R.W and K.G. Porter. 1990. Heterotrophic, autotrophic, and mixotrophic nanoflagellates: seasonal abundances and bacterivory in a eutrophic lake. Limnol. Oceanogr. 35: 1821–1832.

Sanders, R.W., K.G. Porter, S.J. Bennett, and A.E. DeBiase. 1989. Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community. Limnol. Oceanogr. 34: 673–687.

SAS Institute Inc. 1990. SAS user's guide: statistics, Version 6 edition. SAS Institute Inc., Cary, NC. 956 p.

Schindler, D.E. 1992. Nutrient regeneration by sockeye salmon (*Oncorhynchus nerka*) fry and subsequent effects on zooplankton and phytoplankton. Can. J. Fish. Aquat Sci. 49: 2498–2506.

Schlesinger, D.A., L.A. Molot, and B.J. Shuter. 1981. Specific growth rates of freshwater algae in relation to cell size and light intensity. Can. J. Fish. Aquat. Sci. 38: 1052–1058.

Shapiro, J. 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes, p. 105–116. *In* J. Barica and L.R. Mur [ed.]. Hypertrophic ecosystems. Dr. W. Junk, The Hague, The Netherlands.

Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: an ecosystem approach to lake restoration, p. 85–96. *In* P.L. Brezonik and J.L. Fox [ed.]. Proceedings of a Symposium on Water Quality Management Through Biological Control. U.S. Environmental Protection Agency, Washington, D.C.

Shearer, J.A. 1978. Two devices for obtaining water samples integrated over depth. Can. Fish. Mar. Serv. Tech. Rep. 772: 9 p.

Shearer, J.A., E.R DeBruyn, D.R. Clercq, D.W. Schindler, and E.J. Fee. 1985. Manual of phytoplankton primary production methodology. Can. Tech. Rep. Fish. Aquat. Sci. 1341: 58 p.

Shearer, K.D. 1984. Changes in elemental composition of hatchery-reared rainbow trout (*Salmo gairdneri*) associated in growth and reproduction. Can. J. Fish. Aquat. Sci. 41: 1592–1600.

Stainton, M.P., M.J. Capel, and F.A.J. Armstrong. 1977. The chemical analysis of freshwater. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25: 180 p.

Stewart-Oaten, A., J.R. Bence, and C.W. Osenberg. 1992. Assessing effects of unreplicated perturbations: no simple solution. Ecology 73: 1396–1404.

Stewart-Oaten, A., W.W. Murdock, and K.R. Parker. 1986. Environmental impact assessment: "Pseudoreplication" in time? Ecology 67: 929–940.

Swift, M.C. 1976. Energetics of vertical migration in *Chaoborus trivittatus* larvae. Ecology 57: 900–914.

Tezuka, Y. 1990. Bacterial regeneration of ammonium and phosphate as affected by the carbon:nitrogen ratio of organic substrates. Microb. Ecol. 19: 227–238.

Threlkeld, T.S. 1987. Experimental evaluation of trophic-cascade and nutrient-mediated effects of planktivorous fish on plankton community structure. p. 161–173. *In* W.C. Kerfoot and A. Sih [ed.]. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH.

Threlkeld, T.S. 1988. Planktivory and planktivore biomass effects on zooplankton, phytoplankton, and the trophic cascade. Limnol. Oceanogr. 33: 1362–1375.

Vadstein, O., A. Jensen, Y. Olsen and H. Reinertsen. 1988. Growth and phosphorus status of limnetic phytoplankton and bacteria. Limnol. Oceanogr. 33: 489–503.

Vanni, M.J. 1987. Effects of nutrients and zooplankton size on the structure of a phytoplankton community. Ecology 68: 624–635.

Vanni, M.J., and D.L. Findlay. 1990. Trophic cascades and phytoplankton community structure. Ecology 71: 921–937.

Vollenweider, R.A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Tech. Rep. O.E.C.D. Paris Das/CSI/68.27: 182 p.

Phenotypic Divergence of Sea-ranched, Farmed, and Wild Salmon

Ian A. Fleming and Bror Jonsson

Norwegian Institute of Nature Research, Tungasletta 2, N-7005 Trondheim, Norway

and Mart R. Gross

Department of Zoology, University of Toronto, Toronto, ON M5S 1A1, Canada

Fleming, I.A., B. Jonsson, and M.R. Gross. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Can. J. Fish. Aquat. Sci. 51: 2808–2824.

We quantified divergence in phenotype of sea-ranched, farmed, and wild Atlantic salmon (*Salmo salar*) of a common genetic stock (River Imsa, Norway). These first-generation fish were also contrasted with a fifth-generation farmed population (Norwegian commercial strain) and with wild and multigeneration sea-ranched populations of coho salmon (*Oncorhynchus kisutch*). In comparisons using mature Atlantic salmon male parr, cultured juveniles had smaller heads and fins and narrower caudal peduncles and could be distinguished from wild juveniles with 100% accuracy. When juveniles were reared to adulthood in the natural marine environment, some environmentally induced differences due to juvenile hatchery rearing persisted but many disappeared. This was particularly true for head and trunk morphology. Greater adult divergence from the wild state was observed in multigeneration sea-ranched coho salmon, suggesting that evolutionary changes may accumulate with time. Continued farming of salmon juveniles through adulthood increased environmentally induced phenotypic divergence considerably. Both rayed-fin sizes and body streamlining decreased. Fifth-generation Norwegian farmed salmon showed the greatest morphological differences. Both the proportion of a fish's life history and number of generations spent in culture are thus probably important determinants of phenotypic divergence of cultured fish from their wild state.

Nous avons quantifié certaines divergences dans les phénotypes de saumons atlantiques (*Salmo salar*) élevés extensivement en mer, élevés en pisciculture et sauvages appartenant à un même stock génétique (rivière Imsa, Norvège). Ces poissons de première génération ont également été comparés à des saumons élevés en pisciculture de cinquième génération (lignée commerciale norvégienne) ainsi qu'avec des populations de saumons coho (*Oncorhynchus kisutch*) sauvages de même qu'élevés extensivement en mer et renfermant des générations multiples. Les comparaisons faites parmi des tacons mâles matures de saumon atlantique ont révélé que les juvéniles de culture avaient des têtes et des nageoires plus petites et des pédoncules caudaux plus fins, ce qui permet de les distinguer sauvages sans aucune erreur. Chez les juvéniles élevés jusqu'à l'âge adulte dans le milieu marin naturel, on a observé que certaines différences induites par le milieu, attribuables à leur séjour initial en écloserie, persistaient, mais que bon nombre d'entre elles disparaissaient. Cela était particulièrement vrai pour ce qui est de morphologie de la tête et du tronc. Les divergences chez les adultes, par rapport aux saumons à l'était sauvage, étaient plus importantes dans le cas de la population multigénérationnelle de cohos élevés extensivement en mer, ce qui laisse penser qu'il peut y avoir accumulation de changements évolutionnaires avec le temps. On a aussi observé que l'élevage continu de juvéniles en écloserie jusqu'à l'âge adulte accroissait considérablement les divergences phénotypiques induites par le milieu; la taille des nageoires rayonnées diminue et le corps devient moins effilé. Ce sont les saumons norvégiens élevés en pisciculture de quatrième génération qui ont montré les plus grandes différences phénotypiques. Ainsi, tant la durée du séjour des poissons dans les élevages que le nombre de générations passées dans ces derniers déterminent probablement de façon importante les divergences phénotypiques entre poissons de culture et poissons sauvages.

Received October 19, 1992
Accepted May 30, 1994
(J11663)

Reçu le 19 octobre 1992
Accepté le 30 mai 1994

Artificial culture exposes fish to new developmental and evolutionary forces that may shape their phenotype. Salmon, for example, are cultured in large numbers for sea ranching (Isaksson 1988) and farming (Anonymous 1992). Sea-ranched salmon are artificially bred and their eggs and fry are reared in hatcheries until release to the sea as free-ranging smolts. Sea ranching, therefore, has curtailed natural spawning and juvenile freshwater rearing. Like sea-ranched salmon, farmed salmon are hatchery reared as juveniles, but complete their growth to adulthood in sea pens, thus being artificially reared for their entire life. Sea ranching and farming thus impose human-engineered breeding patterns and predator-free, high-density rearing conditions at different stages of the life cycle. Both of these culture regimes have led to the divergence of cultured salmon from their wild phenotype (e.g., Reisenbichler and McIntyre 1977; Leary et al. 1985; Swain and Riddell 1990; see also review by Fleming 1995).

Salmon body form has been greatly affected by culture. Both juveniles (Hjort and Schreck 1982; Taylor 1986; Swain et al. 1991) and adults (Fleming and Gross 1989; Lund et al. 1989) in culture have been shown to have diverged morphologically from their wild phenotypes. Cultured salmon generally have smaller heads and fins and different body

TABLE 1. Collections of Atlantic salmon (m = mature; i = immature).

Year	Population	Fish group	Collection date	Sample size (n) Female	Male	Total
Parr						
1991	Imsa	Wild	Nov. 6–21		17_m	17
	Imsa	Cultured	Nov. 15	24_i	$11_i,15_m$	50
Adults						
1989	Imsa	Wild	Nov. 15–16	5	5	10
	Imsa	Sea ranched	Nov. 15–16	5	5	10
	Imsa	Farmed	Nov. 15–16	19	20	39
1990	Imsa	Wild	Nov. 11	24	24	48
	Imsa	Sea ranched	Nov. 15	22	24	46
	Sunndalsøra	Farmed	Nov. 11	24	24	48
1991	Imsa	Wild	Nov. 7	12	22	34
	Imsa	Sea ranched	Nov. 7	32	27	59

streamlining than wild salmon. The causes of this divergence, however, remain unclear, particularly in adults.

Salmon body form is determined both genetically (Riddell et al. 1981; Taylor and McPhail 1985; Gjerde and Schaeffer 1989; Beacham 1990) and environmentally (Martin 1949; Winans 1984; Currens et al. 1989). Fleming and Gross (1989) proposed that several differences between multigeneration sea-ranched and wild *adult* coho salmon (*Oncorhynchus kisutch*), particularly in body size and depth, snout length, and breeding colouration, may be an evolutionary response to altered selection in culture. They also suggested that altered selection may help explain differences in fin morphology, although its importance relative to other factors, such as environmentally induced changes, was unknown. Swain et al. (1991) found that while genetic divergence in *juvenile* morphology of multigeneration sea-ranched coho salmon exists, the majority of morphological divergence is environmentally induced. They suggested that the environmentally induced divergence established as juveniles, or environmental differences in the use of the marine environment, may explain the divergence in adults found by Fleming and Gross (1989).

The purpose of the present study was to examine the extent of environmentally induced changes to salmon morphology that are potentially important for performance, survival, and success of salmon in nature. We did this by contrasting both juvenile and adult Atlantic salmon (*Salmo salar*) with similar genetic backgrounds but different rearing histories. The salmon were from a common genetic stock in the River Imsa, Norway, and were either wild, sea ranched, or farmed. In addition, the Imsa fish were compared with a fifth-generation strain of the common Norwegian farmed salmon used throughout Norway for aquaculture. Finally, the divergence of single-generation sea-ranched Atlantic salmon from their wild phenotype was contrasted with that of multigeneration sea-ranched coho salmon.

Materials and Methods

Atlantic Salmon

River Imsa parr

Wild parr were collected in the River Imsa, southwestern Norway (58°59′N, 5°58′E), using a fish trap located 100 m above the river outlet (Tables 1 and 2). The River Imsa is a short, 1-km-long river that empties into the Boknafjord near the city of Stavanger. It is characterized by water temperatures ranging from 2 to 3°C in winter to summer maxima of about 20°C. Its discharge ranges from 2 to 3 m^3/s in summer to autumn maxima of about 10 m^3/s, with an annual mean of 5.1 m^3/s (Jonsson et al. 1988). Fifteen to 117 adult Atlantic salmon ascend the river annually to spawn naturally; the number of descending smolts ranges from 477 to 3144 annually (Jonsson and Ruud-Hansen 1985; B. Jonsson et al. 1991). Approximately 82% of male parr mature precociously as 1-yr-olds (Bohlin et al. 1986) and over 90% of the smolts are 2 yr old (Jonsson et al. 1990). A corresponding group of cultured parr were collected from rearing pools at the NINA Research Station located at the mouth of the River Imsa (Tables 1 and 2). This hatchery is supplied with River Imsa water at slightly elevated temperatures that range from 2 to 8°C during the winter to summer maxima of about 20°C. Eggs were incubated in Heath vertical stack incubators with a water flow of 4 L/min and about 1.5 L of eggs per tray. At the onset of feeding the alevins were transferred to 1-m^2 pools with a water depth of 20 cm and a flow of 5.5 L/min. They were fed EWOS food pellets every 10 min during daylight until they reached about 10 cm in length, after which they were fed every 20 min during daylight. In early June, the fish were transferred to 4-m^2 pools with a water depth of 50 cm and a flow of about 40 L/min to grow for the remainder of their first year. About 50% of the juveniles smolted at the end of this period and were either released near the mouth of the River Imsa to produce the sea-ranched adult fish or transferred to saltwater rearing facilities to produce the farmed adult fish. The remainder were held at the hatchery in 12-m^2 pools with a water flow of about 120 L/min until they smolted at the end of their second year. They were then treated the same as the 1-yr smolts. Approximately 70% of male parr in the hatchery matured precociously (Hansen et al. 1989).

Tagging of all wild and cultured smolts with uniquely numbered Carlin tags and records of all adults ascending the River Imsa since salmon culture operations began in 1981 allowed us to estimate the proportional genetic contribution from parents with different rearing histories. For each generation of spawners, both in the river and in the hatchery (see B. Jonsson et al. 1991 for details of spawner

TABLE 2. Mean weight (g) and fork length (cm) (standard deviations in parentheses) of parr and adult Atlantic salmon used in this study (m = mature; i = immature).

Year	Population	Fish group	Female		Male	
			Weight	Fork length	Weight	Fork length
Parr						
1991	Imsa	Wild			36.7_m (14.5)	15.33_m (2.04)
	Imsa	Cultured	30.7_i (11.0)	14.01_i (1.84)	30.6_i (9.8)	14.21_i (1.48)
					25.9_m (19.6)	13.03_m (1.91)
Adults						
1989	Imsa	Wild	1983 (412)	59.04 (3.96)	2448 (673)	64.16 (5.71)
	Imsa	Sea ranched	1746 (156)	57.60 (1.97)	2240 (471)	65.30 (5.24)
	Imsa	Farmed	3317[a] (650)	69.21 (4.51)	2158[b] (456)	63.87 (4.05)
1990	Imsa	Wild	2856 (1669)	64.09 (11.13)	1920 (467)	60.01 (4.12)
	Imsa	Sea ranched	3974 (1749)	72.77 (10.81)	1645 (489)	65.50 (5.11)
	Sunndalsøra	Farmed	3728 (705)	69.13 (3.42)	4008 (793)	74.43 (5.42)
1991	Imsa	Wild	2812 (1798)	64.61 (13.08)	1498 (412)	55.68 (5.13)
	Imsa	Sea ranched	2123 (1455)	58.60 (11.00)	1385 (358)	54.44 (4.64)

[a]10 of 19 males weighed.
[b]9 of 20 females weighed.

numbers), we knew their sex, age, and rearing background (i.e., wild, sea ranched, or farmed). This allowed us to back-calculate an estimate of the genetic contribution to each generation based on each sex contributing half of the genes, on knowledge of the smolt age structure, and on the assumption that all fish were equally capable of contributing genes independent of their origin.

Both groups of parr, cultured and wild, were derived from a common genetic pool of the River Imsa population and thus had similar genetic backgrounds (Table 3), resulting from the intermixing of sea-ranched and wild spawners both in the river and in the hatchery. For instance, 10% of the genes of wild parr and 4% of those of cultured parr in 1991 were estimated to have been contributed by parental lineages that had been only reared in the wild. Similarly, 32% of the genes of wild parr and 43% of those of cultured parr were estimated to have been contributed by parental lineages that had been wild reared three generations ago, but sea ranched during the past two generations.

Mature male parr were identified by free-flowing milt. Immature cultured parr were sexed after measurement by internal examination of gonads. A single immature wild-reared parr was released.

River Imsa adults

All adults had similar genetic backgrounds within years, but differed somewhat across years, based on calculations incorporating age structure at smoltification and sea-age-at-maturity (Table 3). For example, the proportional genetic contribution of pure wild parental lineages to the wild and sea-ranched adults studied was similar within years, but decreased across years. The one exception to this pattern of genetic similarity within years was the farmed adults of 1989, which were of predominantly pure wild lineage with a small proportion of single-generation farmed lineage and, in contrast with the wild and sea-ranched adults of the same year, had no sea-ranched lineage.

Wild fish, derived from adults that spawned naturally in the River Imsa during November and December, completed their entire life cycle in the wild. The embryos incubated through the winter in gravel nests, emerging the following April. After 2 yr in the river, most juveniles migrated to the Norwegian Sea where most of their growth to maturity occurred. Eighty-three percent (n = 76) of the fish had attained sexual maturity after one winter at sea, 15% (n = 14) after two winters, and 2% (n = 2) after three winters (cf. B. Jonsson et al. 1991). They ascended the River Imsa during July through November to spawn. Typically in the river, less than 10% of the spawners, primarily females, survive to spawn another year (N. Jonsson et al. 1991).

Sea-ranched fish, hatchery reared as juveniles to smoltification before being released at the outlet of the River Imsa to migrate to sea, completed the remainder of their growth to adulthood naturally. Their experience in the marine environment was similar to that of the wild adults. Sea-ranched salmon followed the same migratory routes to the feeding grounds and exploited the same areas of the North Atlantic as the Imsa wild salmon (Hansen and Jonsson 1991). Their sea-age-at-maturity was also similar, as 80% (n = 92) of the sea-ranched adults had matured following their first

TABLE 3. Background of parr and adult Atlantic salmon from the River Imsa used in this study, estimated as the proportional genetic contribution from parental lineages having different rearing histories (see Materials and Methods). Three generations of rearing history are shown, prior to which all fish were of wild origin. Arrows indicate the sequential progression of generations.

		Parental lineage (rearing history)						
Year	Fish Group	Wild ↓ Wild ↓ Wild	Wild ↓ Sea ranched ↓ Wild	Wild ↓ Wild ↓ Sea ranched	Sea ranched ↓ Wild ↓ Sea ranched	Wild ↓ Sea ranched ↓ Sea ranched	Sea ranched ↓ Sea ranched ↓ Sea ranched	Wild ↓ Wild ↓ Farmed
Parr								
1991	Wild	0.101	0.129	0.224	0.061	0.324	0.161	0.0
	Cultured	0.037	0.063	0.032	0.152	0.428	0.287	0.0
Adults								
1989	Wild	0.365	0.0	0.635	0.0	0.0	0.0	0.0
	Sea ranched	0.281	0.0	0.719	0.0	0.0	0.0	0.0
	Farmed	0.918	0.0	0.0	0.0	0.0	0.0	0.082
1990	Wild	0.156	0.161	0.469	0.0	0.214	0.0	0.0
	Sea ranched	0.088	0.145	0.468	0.0	0.299	0.0	0.0
1991	Wild	0.027	0.079	0.531	0.0	0.363	0.0	0.0
	Sea ranched	0.016	0.092	0.591	0.0	0.301	0.0	0.0

winter at sea, 19% (n = 22) following their second, and 1% (n = 1) following their third. Return migrations to the Norwegian coast occurred concurrently, although the wild salmon tended to ascend the River Imsa earlier than sea-ranched salmon (B. Jonsson et al. 1991). All wild and sea-ranched adults ascending the River Imsa from the sea were captured in the fish trap during July through October of 1989 through 1991 (Tables 1 and 2). From the trap, which was checked daily, fish were transferred to 72-m^2 freshwater pools at the research station and held until mature.

Farmed fish were transferred as 1-yr-old smolts from the NINA Research Station in 1987 to net pens and raised to maturity under farming conditions at the Høgsfjord Edelfisk farm (59°03′N, 5°58′E). Located within the Boknafjord, the farm is about 5 km away by sea from the River Imsa. Salinity at this location is approximately 30‰ and water temperatures range from 4°C in winter to 16°C in summer. The net pens were 250 m^3 and approximately 20 m above the sea floor. Fish were fed Skretting food pellets every 20 min during daylight and reared at a density of approximately 15–20 kg/m^3. In August 1989 the fish were transferred back to the NINA Research Station and sexual maturation was completed in 72-m^2 freshwater pools (Tables 1 and 2).

Sunndalsøra adults

These fish were the fifth generation of farmed salmon from the selection program at Sunndalsøra, Norway (Gjedrem et al. 1991). Over 80% of Norwegian farmed salmon used in the commercial industry originate from this program. The strain we studied was developed in 1971 from 18 different Norwegian populations and had since been subjected to directed selection for high growth rate and low incidence of grilse (i.e., maturity after one sea winter). By the third generation, the strain was dominated by fish derived from the River Namsen (>70%) and only six of the original populations were still represented (Gjedrem et al. 1991). In 1988, eyed eggs from Sunndalsøra were transported to Hestå Bruk hatchery for freshwater rearing, and then the half-year smolts to the Riska Fisk farm (59°02′N, 5°49′E) for saltwater rearing. The Riska Fisk farm is located within the Boknafjord and about 17 km by sea from the River Imsa and 13 km beyond the Høgsfjord farm. Salinity and temperature conditions at Riska Fisk were similar to those at the Høgsfjord farm. Net pens, however, were twice the size of those at Høgsfjord (500 m^3) and higher above the sea floor (50 m). As at Høgsfjord, Riska Fisk salmon were fed Skretting food pellets every 20 min during daylight, but were reared at slightly higher densities (approximately 25 kg/m^3). In August 1990, a collection of Riska Fisk adults were transported to the NINA Research Station where sexual maturation was completed in 72-m^2 freshwater pools (Tables 1 and 2).

Morphometric Measurements

Parr were anaesthetized with tricaine methanesulfonate (MS 222), weighed (±0.01 g), and their left sides photographed against a horizontal light-blue background using a Nikon FA 35-mm camera with a Nikkor 55-mm macrolens and ring flash. A millimetre ruler was set at a fixed position directly below the lens. Adults of a similar state of maturity (males: gametes readily extruded; females: bellies soft) were anaesthetized with MS 222, fork length measured (±1 mm), damage to the mouth scored, and photographed. Damage to the kype and jaws, including wounds and distortion in their shape, and distortion in the angle of the jaws with respect to each other were scored increasingly from 1 to 3 (1 = no evident damage or distortion, 2 = minor, 3 = extreme). In 1989, each fish was placed into a narrow aquarium and photographed using a Minolta Maxum 7000 35-mm camera with a 35- to 110-mm zoom lens set at 50–60 mm and a camera-mounted flash. Because fish sometimes rested on the aquarium bottom, distorting their ventral surface, adults in 1990 and 1991 were photographed like the parr except for the use of two studio lamp flashes.

The photographs were digitized using a computer graphics tablet. Adipose and caudal fin areas and spatial coordinates of 23 adult and 19 parr landmarks were recorded (Fig. 1). From these landmark coordinates, both conventional (e.g., Hubbs and Lagler 1947) and truss measurements (Strauss and Bookstein 1982) were calculated.

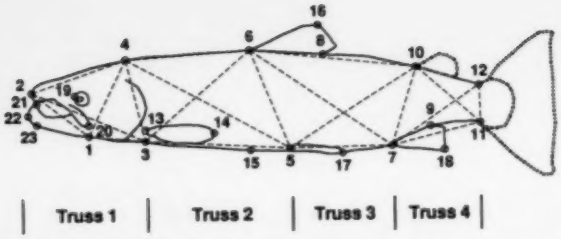


FIG. 1. Location of the 23 morphometric landmarks (points), 21 trusses (dashed lines), and two fin areas (dotted lines). Landmarks are described by Winans (1984), except dorsal point at least depth of caudal peduncle (12), origin of pectoral fin (13), distal tips of pectoral (14), dorsal (16), pelvic (17), and anal fins (18), point on ventral surface of body directly below anterior dorsal fin origin (15) and ventral point on lower jaw directly below kype tip (23), both based on a line drawn perpendicular to the horizontal axis of the fish, anteriormost edge of orbit (19), posterior tip of maxillary (20), and dorsalmost (21) and anteriormost points of kype (22). Landmarks 20–23 were not measured on parr. The body was divided into four regions (head, anterior trunk, posterior trunk, and tail) to localize morphological features.

Statistical Analyses

Adult morphology was analyzed separately for the two sexes because of sexual dimorphism. Due to the ventral surface problem in the 1989 adult photographs, the data were analyzed both without these adults and with them but excluding landmarks 3, 5, 7, and 15 (the "reduced character set"). Centroid size, the sum of squared distances between all pairs of marginal landmark coordinates (i.e., excluding points 13, 14, and 16–23), was used as a multivariate measure of adult and parr body size (Bookstein 1990; Ehlinger 1991). But because centroid size could not be accurately calculated for the 1989 fish, fork length, which is highly correlated with centroid size (females: $r = 0.997$, $n = 118$, $P < 0.001$; males: $r = 0.994$, $n = 127$, $P < 0.001$), was used as the measure of body size when analyzing the reduced character set.

All morphometric measures were first log-transformed and standardized to mean = 0 and standard deviation = 1. Characters were then size adjusted and transformed into shape variates by expressing them as residuals from the regression line describing the relationship between the character and the body size measure (centroid size or fork length). Because of heterogeneity of size–character relationships, the common within-groups slope for each character was used for size adjustment (Thorpe 1983; Reist 1986). It is a more satisfactory method of size adjustment than pooled group, or individual within-group slopes, even where heterogeneity in size–character slopes exist (Reist 1986). To insure our results were not biased by our method of size adjustment, we contrasted the results from the residual method with those from the sheared principal component and the Burnaby methods (Rohlf and Bookstein 1987; programs written by N. MacLeod (Rohlf and Bookstein 1990)). Because all three methods led to the same conclusions, the results were independent of the procedure of size adjustment, and only those from the residual method are presented.

Differences among fish groups in univariate morphological characters were examined by analysis of variance (ANOVA), with fish group and year as effects. Because of univariate testing of multiple characters, significance levels of effects were adjusted by sequential Bonferroni tests (Rice 1989). When a morphological character was found to exhibit a significant among-fish-group effect, pairwise comparisons between fish groups for that character were tested with Scheffé's multiple comparison method (Kleinbaum and Kupper 1978).

Principal components analysis was used to objectively describe the pattern of similarities and differences among individuals of the various fish groups, without a priori knowledge of group membership. It reduces the dimensions of the data to a few principal components, which are linear combinations of the original variables, to allow a joint study of their interrelationships. This procedure was conducted using the correlation matrix of the size-adjusted data. Linear discriminant function analysis was used to (1) differentiate among fish groups and (2) classify individuals to fish group based on a priori knowledge of relationships among fish groups. In contrast with principal components analysis, discriminant analysis uses knowledge of the group and proceeds to maximize the amount of multivariate variation of across-group means relative to within-group variation. Individuals were classified to fish group using a jackknife procedure (BMDP: Dixon 1981). This involves leaving out each individual in turn, calculating a discriminant function based on the remaining $n - 1$ individuals, and then classifying the left-out individual.

We also assessed contributions of environmentally induced changes to salmon morphology that may be ascribed solely to developmental influences of culture (e.g., temperature, food availability). To do this, principal components and discriminant analyses were also run excluding morphological characters susceptible to physical damage (jaw and fin length, height and area measurements). These analyses provide a conservative estimate of developmental influences of culture, since potential developmental effects on characters susceptible to physical damage have been excluded. Analyses were performed with the Statistical Package for the Social Sciences (version SPSS/PC) unless otherwise indicated.

Coho salmon

The divergence of single-generation sea-ranched from wild Atlantic salmon was contrasted with that of multigeneration sea-ranched from wild coho salmon. Coho salmon data for 12 morphological characters (body length, depth and colouration, snout length, caudal peduncle depth, pectoral, pelvic and adipose fin lengths, and dorsal and anal fin heights and bases; described in Fleming and Gross 1989) were derived from Fleming and Gross (1989; five sea-ranched and 12 wild populations, $n = 368$ females with a complete character set), Fleming and Gross (1994; one sea-ranched and one wild population, $n = 75$ females), and Fleming (unpublished data; two sea-ranched (Skagit and Big Qualicum hatcheries) and one wild population (Black Creek), $n = 77$ females). All characters were size adjusted to the mean postorbital–hypural body length of all females (498 mm), except body length itself, using the same procedure described earlier for Atlantic salmon. Euclidean distances, a measure of dissimilarity (Pimentel 1979), between pairs of populations were calculated to examine morphological affinities and analysis of covariance (ANCOVA) tested for differences between sea-ranched and wild populations, while controlling for geographic distances among them. Character differences between sea-ranched and wild populations were

examined by nested ANOVA, with females nested within population, and geographical region (lower mainland of British Columbia, Puget Sound, and Vancouver Island) as an effect. To directly contrast results from the sea-ranched versus wild comparison using Atlantic salmon females with those using coho salmon females, discriminant analysis was conducted on each of the two data sets, using only characters common between them (i.e., body size and depth, snout length, caudal peduncle depth, and pectoral, pelvic, dorsal, anal, and adipose fin measurements). For coho salmon, residuals from univariate ANOVAs comparing morphology among geographical regions were used to control for geographical effects in discriminant analysis. To compare the discriminant classification accuracies of Atlantic and coho salmon, the chance-corrected classification statistic, Cohen's kappa (Titus et al. 1984), was used.

Results

Parr

Immature and mature cultured males and females

Immature male and female parr did not differ in their morphology (discriminant analysis, $F_{18,48} = 0.87$, $P = 0.611$) (Fig. 2; Table 4). In contrast, mature male parr differed significantly from immature male and female parr (Fig. 2; Table 4). Mature males had longer and deeper heads, longer pectoral fins, and deeper bodies and caudal peduncles (Appendix 1). Mature and immature parr were classified by discriminant analysis with 100% accuracy.

Results were relatively unaltered by excluding characters susceptible to physical damage (fin lengths, heights, and areas). The only change was a drop in the classification accuracy of immature male and female parr from 69 to 63%.

Cultured and wild mature males

Mature cultured males differed significantly in morphology from mature wild males (Fig. 2; Table 4). Significant differences existed in 45% of the morphological characters measured (14 of 31 characters; Appendix 1). Cultured males had smaller heads and fins and a narrower caudal peduncle than wild parr. Differences also existed in anterior and posterior regions of the trunk, with cultured males tending to have larger measurements in the posterior region than wild parr. Mature males were classified as cultured or wild with 100% accuracy by discriminant analysis, even when characters susceptible to physical damage were excluded.

Adults

Sea-ranched and wild Atlantic salmon

There was significant variation in adult morphology among years. Twenty-four percent of the female and 27% of the male morphological characters varied significantly among years (both sexes: kype height, adipose and caudal fin areas, and trusses 2–4, 1–4, 4–5, 5–10, and 7–12; males: truss 3–6).

While the morphology of sea-ranched and wild adults overlapped across years (Fig. 3 and 4), distinct differences between the two groups existed. Significant differences in principal component scores occurred across PC3, explaining 8.1–11.6% of the variance (Tables 5 and 6). Of the 33 characters examined, sea-ranched and wild females differed in 12% (4) and males in 15% (5) (Appendices 2 and 3). Sea-ranched adults had reduced dorsal fin height relative to wild adults. Additional differences unique to each sex also existed. Sea-ranched females had a longer horizontal truss in the anterior trunk region and a shorter horizontal truss, as well as a shorter oblique truss in the posterior trunk region than wild females. Sea-ranched males had shorter pectoral, narrower dorsal and smaller caudal fins, and shallower heads than wild males. Damage to the kype and jaws was infrequent and there were no differences between sea-ranched and wild fish of either sex (Table 7).

Classification accuracy to sea-ranched or wild by discriminant analysis was 81% for females and 88% for males using

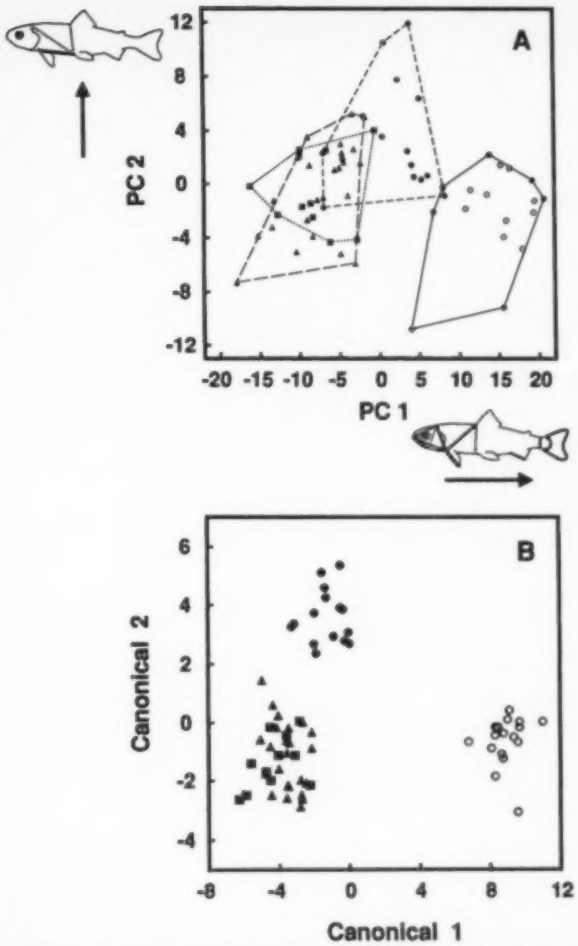


FIG. 2. (A) Principal components analysis and (B) discriminant function analysis of parr morphology using size-adjusted data. Scores for cultured females are solid triangles, immature cultured males are solid squares, mature cultured males are solid circles, and mature wild males are open circles. In Fig. 2A, characters important in describing the pattern of morphological variation, and thus have high loadings on a PC are diagrammed on the fish outlines (loadings: solid lines, 0.80–1.00; dotted lines, 0.60–0.79). Arrows indicate the direction of correlation between the characters and the PC. (A complete set of character loadings on principal components and of standardized canonical discriminant function coefficients may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada)

TABLE 4. Means and ANOVA of principal component scores[a] for parr. All significantly different groups based on pairwise comparisons (Scheffé's method; $P < 0.05$) are given in parentheses below each component score.

Principal Component	Cultured: Female immature (C_{fi})	Cultured: Male immature (C_{mi})	Cultured: Male mature (C_{mm})	Wild male mature (W_{mm})	ANOVA $F_{3,63}$	ANOVA P
PC1	−7.37 (C_{mm}, W_{mm})	−8.33 (C_{mm}, W_{mm})	1.61 (C_{fi}, C_{mi}, W_{mm})	14.38 (C_{fi}, C_{mi}, C_{mm})	90.88	<0.001
PC2	−0.46 (C_{mm})	−0.49	3.48 (C_{fi}, W_{mm})	−2.11 (C_{mm})	6.98	<0.001
PC3	−0.2580	−0.1090	1.2383	−0.6579	1.06	0.372

[a]A complete set of character loadings on principal components may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

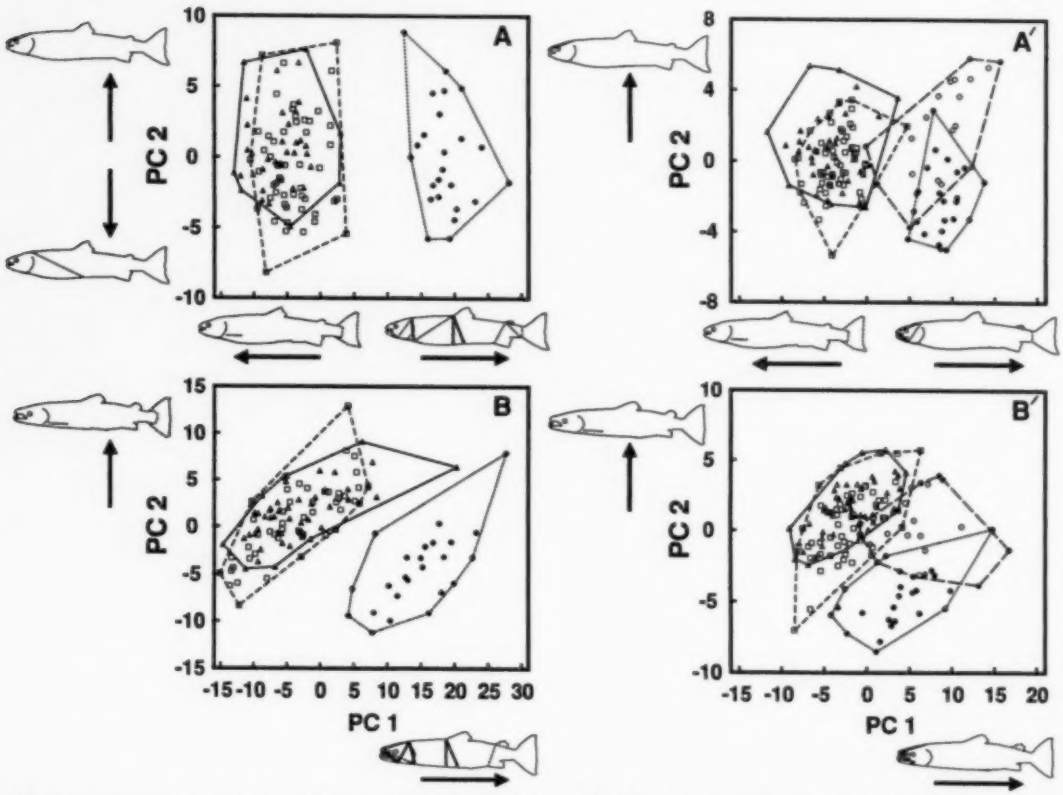


FIG. 3. Principal components analysis of the size-adjusted morphology of adult Atlantic salmon using the full (female = A, male = B) and reduced (female = A′, male = B′) character sets (see Materials and Methods). PC scores for wild Imsa adults are solid triangles, sea-ranched Imsa adults are open squares, farmed Imsa adults are open circles, and farmed Sunndalsøra adults are solid circles. Characters loading highly on each PC are diagrammed on the fish outlines (loadings: solid lines, 0.80–1.00; dotted lines, 0.60–0.79), with arrows indicating the direction of correlation. (A complete set of character loadings on principal components may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada)

all morphological characters (see Materials and Methods; all misclassifications were between the two fish groups; Fig. 4). Exclusion of characters susceptible to physical damage resulted in a decrease in the Mahalanobis distance between the population means (female: from $D^2 = 5.77$ to 2.53; male: from $D^2 = 7.42$ to 4.60) and a subsequent decrease in classification accuracy to 70% for females and 79% for males. When using only characters congruent with those examined in female coho salmon, classification accuracy declined further to 60% for females ($D^2 = 1.04$) and 65% for males ($D^2 = 1.90$). This

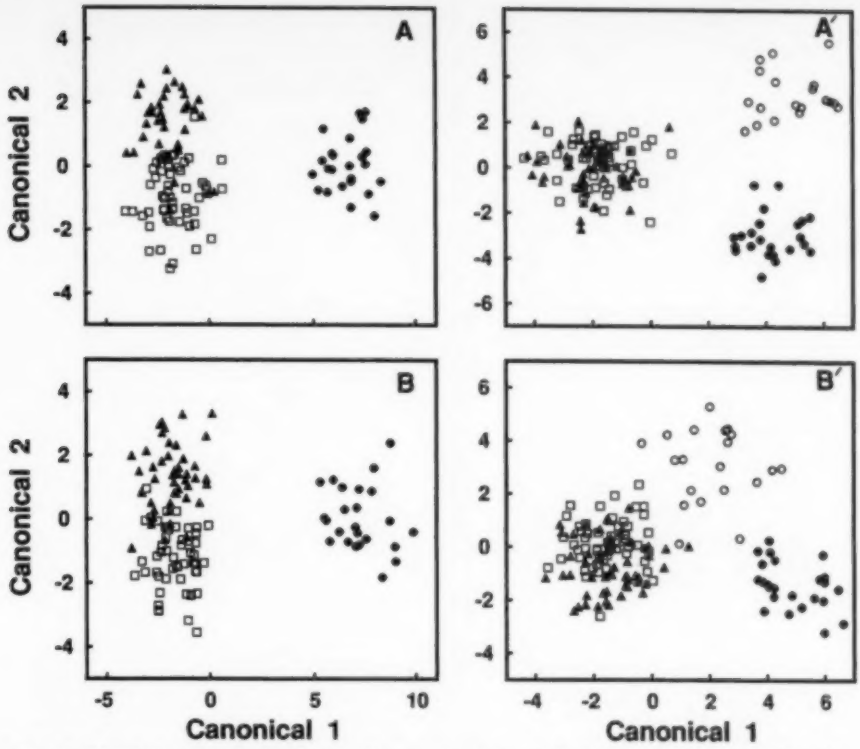


FIG. 4. Discriminant analysis of size-adjusted morphology of adult Atlantic salmon using the full (female = A, male = B) and reduced (female = A′, male = B′) character sets. Canonical function scores for wild Imsa adults are solid triangles, sea-ranched Imsa adults are open squares, farmed Imsa adults are open circles, and farmed Sunndalsøra adults are circles. (A complete set of standardized canonical discriminant function coefficients may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada)

was equivalent to a classification accuracy of 17% better than expected by chance alone for females (kappa = 0.167) and 30% for males (kappa = 0.298). If, in addition, congruent characters susceptible to damage were excluded, classification accuracy drops further to 52% for females (D^2 = 0.06, kappa = 0) and 63% for males (D^2 = 1.06, kappa = 0.258).

Only three of the 14 characters that differed between cultured and wild mature male parr persisted in adult males: shorter pectoral and dorsal fins, and a smaller caudal fin in sea-ranched than wild males. There was also persistence of shallower bodies in the head region of cultured relative to wild males, although the actual location of this difference shifted from head depth 2 in mature male parr to head depth 1 in adult males.

Sea-ranched and wild coho salmon

Comparison of eight multigeneration sea-ranched to 14 wild populations of female coho salmon from British Columbia, Canada, and Washington State, USA, revealed distinct differences between the two groups. Pairwise euclidean distances among wild populations ($\bar{x}$ = 3.95, n = 91, SE = 0.12) were less than those among sea-ranched populations ($\bar{x}$ = 4.93, n = 28, SE = 0.26), which were, in turn, less than those between sea-ranched and wild populations ($\bar{x}$ = 5.34, n = 112, SE = 0.13; $F_{2,227}$ = 25.35, P < 0.001, covariate geographical distance $F_{1,227}$ = 33.60, P < 0.001). Sea-ranched coho salmon females differed from wild females in 50% of the characters examined (6 of 12, using Bonferroni sequentially adjusted significance levels). Like sea-ranched Atlantic salmon, they had significantly shorter dorsal fin heights ($F_{1,16}$ = 13.66, P = 0.002) and pectoral fin lengths ($F_{1,16}$ = 40.59, P < 0.001) than their wild counterparts. In addition, sea-ranched coho females had significantly smaller kypes ($F_{1,16}$ = 59.71, P < 0.001), anal fin bases ($F_{1,16}$ = 17.40, P = 0.001), pelvic fin lengths ($F_{1,16}$ = 19.98, P < 0.001), and less intense red colouration ($F_{1,16}$ = 13.27, P = 0.002) than wild females. There were also significant regional differences in body length ($F_{2,16}$ = 9.65, P = 0.002), kype ($F_{2,16}$ = 24.34, P < 0.001), anal fin height ($F_{2,16}$ = 7.60, P = 0.005), dorsal fin height ($F_{2,16}$ = 12.53, P < 0.001), base ($F_{2,16}$ = 14.38, P < 0.001), adipose ($F_{2,16}$ = 17.83, P < 0.001), and pelvic fin lengths ($F_{2,16}$ = 12.08, P < 0.001).

Sea-ranched and wild female coho salmon could be classified by discriminant function analysis, controlling for regional effects, with 73% accuracy (Mahalanobis distance between the groups D^2 = 2.18) using the 11 characters congruent with those examined in Atlantic salmon (i.e., body colouration excluded). This was equivalent to a classification accuracy of 43% better than expected by chance alone

TABLE 5. Means and ANOVA of principal component scores[a] for adult Atlantic salmon (females, df = 2,109; males, df = 2,116) using all measured characters. Year effects and year-by-fish group interactions were included in analyses. All significantly different groups based on pairwise comparisons (Scheffé's method; $P < 0.05$) are given in parentheses below each component score.

Sex	Principal component	River Imsa		Sunndalsøra farmed (F)	ANOVA	
		Wild (W)	Sea ranched (SR)		F	P
Females	PC1	−6.03 (F)	−4.23 (F)	18.56 (W, SR)	322.31	<0.001
	PC2	0.72	−0.50	0.05	1.01	0.367
	PC3	−1.18 (SR)	0.83 (W)	−0.11	3.55	0.032
Males	PC1	−3.64 (F)	−3.58 (F)	14.58 (W, SR)	61.49	<0.001
	PC2	1.52 (F)	0.74 (F)	−4.49 (W, SR)	21.96	<0.001
	PC3	0.88 (SR)	−0.99 (W)	0.42	4.01	0.021

[a]A complete set of character loadings on principal components may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

TABLE 6. Means and ANOVA of principal component scores[a] for adult Atlantic salmon (females, df = 3,135; males, df = 3,143) using a reduced character set that excludes ventral landmarks. Year effects and year-by-fish group interactions were included in analyses. All significantly different groups based on pairwise comparisons (Scheffé's method; $P < 0.05$) are given in parentheses below each component score.

Sex	Principal component	River Imsa			Sunndalsøra farmed (F_s)	ANOVA	
		Wild (W_i)	Sea ranched (SR_i)	Farmed (F_i)		*F*	*P*
Females	PC1	−4.17 (F_i, F_s)	−3.46 (F_i, F_s)	8.78 (W_i, SR_i)	8.68 (W_i, SR_i)	135.16	<0.001
	PC2	0.56 (F_s)	−0.13 (F_i, F_s)	2.01 (SR_i, F_s)	−2.23 (W_i, SR_i, F_i)	12.94	<0.001
	PC3	0.30 (F_i)	-0.39 (F_s)	−0.99 (W_i, F_s)	1.23 (SR_i, F_i)	3.97	0.009
Males	PC1	−1.86 (F_i, F_s)	−2.02 (F_i, F_s)	5.92 (W_i, SR_i)	3.73 (W_i, SR_i)	16.17	<0.001
	PC2	1.54 (F_s)	0.56 (F_s)	0.21 (F_s)	−4.76 (W_i, SR_i, F_i)	45.50	<0.001
	PC3	0.75 (SR_i, F_i)	−0.76 (W_i, F_s)	−1.63 (W_i, F_s)	1.54 (SR_i, F_i)	7.48	<0.001

[a]A complete set of character loadings on principal components may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

(kappa = 0.429). If characters susceptible to physical damage are excluded, overall classification accuracy falls to 68% ($D^2 = 1.19$, kappa = 0.323).

Farmed and wild Atlantic salmon

The morphology of Imsa farmed and wild adults differed considerably (Fig. 3 and 4; Table 6). Much of this difference was summarized by the first principal component. Of the 19 characters examined (reduced character set, ventral landmarks excluded; see Materials and Methods), farmed and wild Imsa females differed in 74% (14) and males in 53% (10) (Appendices 2 and 3). Farmed Imsa adults had a longer head, smaller rayed fins, a larger adipose fin, and shorter horizontal trusses in the trunk region. Both sexes of farmed Imsa adults also had significantly more distorted jaws and farmed males more damage to their kypes and jaws than their wild counterparts (Table 7), which were almost free of such effects. Imsa farmed and wild adults could be distinguished with 100% accuracy (female $D^2 = 56.66$; male $D^2 = 22.52$). Exclusion of characters susceptible to physical damage resulted in a decrease in Mahalanobis distance between the population means (female $D^2 = 18.49$; male $D^2 = 8.38$) and a decline in classification accuracy for males to 93%, but not for females.

Six of eight character differences between cultured and wild mature male parr persisted between wild and farmed male adults of the Imsa population. All but one of these characters, a horizontal truss in the anterior trunk region,

TABLE 7. Mean ranking of increasing damage to the kype and jaws and distortion in the angle of the jaws with respect to each other in adult Atlantic salmon (females, $n = 143$; males, $n = 151$) and analyses from Kruskal–Wallis one-way ANOVAs. All significantly different groups based on pairwise comparisons (Mann–Whitney U-tests adjusted for multiple comparisons by sequential Bonferroni tests: $P < 0.05$) are given in parentheses below each mean ranking.

Character	Sex	River Imsa			Sunndalsøra farmed (F_s)	Kruskal–Wallis one-way ANOVA	
		Wild (W_i)	Sea ranched (SR_i)	Farmed (F_i)		χ^2	P
Kype	Female	70.50	72.92	78.13	70.50	6.22	0.101
	Male	65.07 (F_i, F_s)	63.25 (F_i, F_s)	99.70 (W_i, SR_i)	105.65 (W_i, SR_i)	25.09	<0.001
Jaws	Female	61.52	73.27	82.92	81.56	7.73	0.052
	Male	56.38 (F_i, F_s)	62.04 (F_i, F_s)	108.10 (W_i, SR_i)	119.58 (W_i, SR_i)	63.04	<0.001
Jaw angle	Female	67.50 (F_i, F_s)	71.16	78.87 (W_i)	79.50 (W_i)	9.20	0.027
	Male	69.00 (F_i, F_s)	67.50 (F_i, F_s)	90.00 (W_i, SR_i)	95.63 (W_i, SR_i)	36.36	<0.001

involved fin morphology. The relative magnitudes of the fin differences were similar to those in parr (range of relative difference between cultured and wild mature male parr: 10–15%; adult males: 6–12%), except for the dorsal fin (relative difference in mature male parr: 13%; adult males: 28%).

There was considerable similarity between farmed adults from Sunndalsøra and those from Imsa in the way they differed from wild adults of the River Imsa (Fig. 3 and 4; Tables 5 and 6). Sunndalsøra farmed adults, like their Imsa counterparts, were less streamlined and had longer heads, smaller rayed fins, and larger adipose fins (Appendices 2 and 3) than the wild adults and could be distinguished with 100% accuracy by discriminant analysis (female $D^2 = 84.50$; male $D^2 = 78.26$). Classification was unaltered using the reduced character set, although Mahalanobis distance dropped (female $D^2 = 61.99$; male $D^2 = 54.94$). Similarly, the exclusion of characters susceptible to physical damage decreased the Mahalanobis distance between population means (female $D^2 = 31.38$; male $D^2 = 23.27$), but not the classification accuracy. Overall, Sunndalsøra farmed and Imsa wild females differed in 79% (26) and males in 64% (21) of the 33 characters examined (full character set; see Materials and Methods).

Sea-ranched and farmed Atlantic salmon

Like wild adults, the morphology of sea-ranched adults from the River Imsa differed considerably from that of farmed adults of Imsa and of Sunndalsøra (Fig. 3 and 4; Tables 5 and 6). Of the 19 characters examined (reduced character set), Imsa sea-ranched and farmed females differed in 84% (16) and males in 53% (10) (Appendices 2 and 3). Similarly, Imsa sea-ranched and Sunndalsøra farmed females differed in 76% (25) and males in 61% (20) of the 33 characters measured (full character set). Like wild adults, sea-ranched adults had a more streamlined body, shorter head, larger rayed fins, and a smaller adipose fin than both Imsa and Sunndalsøra farmed adults. Furthermore, sea-ranched males had less damage to their jaws and kype and less distortion to their jaws than both groups of farmed males (Table 7). Sea-ranched and farmed females of the River Imsa were distinguished by discriminant analysis with 100% accuracy ($D^2 = 62.53$), while males were distinguished with 98% accuracy ($D^2 = 25.25$). Exclusion of characters susceptible to physical damaged did not alter this accuracy for females ($D^2 = 29.00$), but did for males, as it declined to 91% ($D^2 = 8.67$). Similarly, the Imsa sea-ranched adults could be distinguished readily from Sunndalsøra farmed adults (100% accuracy; female $D^2 = 72.83$, male $D^2 = 94.28$). Use of the reduced character set did not alter classification accuracy, but did cause a decrease in Mahalanobis distance (female $D^2 = 64.56$; male $D^2 = 60.72$), and results were altered only slightly further by exclusion of characters susceptible to physical damage (female: accuracy = 99%, $D^2 = 31.38$; male: accuracy = 100%, $D^2 = 35.84$).

Imsa farmed and Sunndalsøra farmed Atlantic salmon

The morphology of Imsa and Sunndalsøra farmed fish also differed (Fig. 3 and 4). Most of the differences were summarized by principal components 2 and 3 (Table 6). Of the 19 characters measured, Imsa and Sunndalsøra farmed females differed in 42% (8) and males in 37% (7) (Appendices 2 and 3). Sunndalsøra adults had shorter paired fins and kype, a deeper head, and a longer horizontal truss in the posterior trunk region. In addition, Sunndalsøra females had a shorter anal fin, forehead length ,and oblique truss in the head region, while males had a longer anal fin and oblique truss in the tail region and a shorter lower jaw than their Imsa counterparts. Both groups of farmed adults incurred similar levels of damage to the kype and jaws, as well as distortion to the jaws (Table 7). Only a single individual, a male, was misclassified by discriminant analysis as belonging to the other farm strain (female $D^2 = 117.90$, male $D^2 = 22.69$). Exclusion of characters susceptible to physical damage did not alter the classification accuracy (female $D^2 = 26.19$, male $D^2 = 10.77$).

Discussion

The body form of Atlantic salmon changes extensively from the wild type within a single generation of culture. Cultured juveniles have smaller heads and fins and narrower caudal peduncles than wild juveniles. A similar divergence has been observed between cultured and wild juvenile coho salmon (Taylor 1986; Swain et al. 1991). There are several

possible explanations for this divergence of cultured juveniles from their wild body form. First, the phenotype of salmon may have evolved to be malleable during ontogeny as an adaptive response to local environmental conditions, and as a consequence the changes seen reflect adaptive adjustment. Second, the changes may be a result of an adaptive ontogenetic mechanism, but the changes are nonadaptive due to the novel environment experienced in culture. In either case, morphological plasticity is common in salmonid fishes (Martin 1949; Currens et al. 1989; Beacham 1990) and has been suggested to be the principle cause of the morphological divergence of cultured from wild salmon (Swain et al. 1991). Third, damage incurred during hatchery rearing from abrasion, disease (Soderberg and Meade 1987), and intraspecific aggression (Abbott and Dill 1985), particularly to fins, may be an equally, or more important, cause than phenotypic plasticity. Fin erosion is found in most fish held in confined rearing facilities (Novotny 1980; Moring 1982; Hansen et al. 1987). Finally, selective mortality, particularly of wild juveniles that can experience over three times the mortality rate of cultured juveniles (Waples 1991; Jonsson and Fleming 1993), might generate the morphological differences. If this were the case, however, the distribution of wild juvenile phenotypes should be a subset of cultured juvenile phenotypes. Because a large proportion of wild juveniles had phenotypes more extreme than cultured juveniles, this explanation does not seem likely (see also Swain et al. 1991). Thus, the morphological differences between cultured and wild juveniles that arise during ontogeny probably reflect phenotypic responses to their different environments, as well as physical damage in culture, and are less an effect of selective mortality.

Phenotypic divergence of cultured from wild juveniles will almost certainly affect their success in the wild. For instance, lifetime damage to fins from juvenile hatchery rearing (e.g., sea-ranched fish) can reduce survivorship (Johansson 1981) and may explain, in part, the more than twofold lower marine survival of cultured than wild juveniles of the River Imsa (B. Jonsson et al. 1991).

Swain et al. (1991) hypothesized that (1) environmental differences established in juveniles and (2) environmental differences between adults in the marine environment could explain the morphological differences found by Fleming and Gross (1989) in mature adults. Our results provide some support for this hypothesis. Four of 14 differences between cultured and wild juveniles that arose during ontogeny persisted and were found in mature adults after natural rearing in the sea for a year or more. One was related to body form and the remaining three to fin morphology: reduced head depth, pectoral and dorsal fin lengths, and caudal fin area in sea-ranched fish. The reduced fin characteristics may have resulted, in part, from fin erosion incurred as juveniles in culture that caused lifelong damage (also Lund et al. 1989). The magnitude of fin differences among adults, however, was less than among juveniles, suggesting that some convergence on a wild phenotype had occurred, possibly through fin regeneration.

There was little evidence that marine environmental differences between sea-ranched and wild adults influenced morphology. A significantly narrower dorsal fin base in sea-ranched than in wild males was the only character difference observed between adults that was not observed in juveniles, although, even here, cultured and wild juveniles did exhibit a nonsignificant trend in the same direction. The lack of environmentally induced differences during natural marine rearing reflects the similarity of environmental experiences by sea-ranched and wild adults in the sea (Hansen and Jonsson 1991). The higher percentage of character differences and greater discrimination of multigeneration sea-ranched from wild coho salmon females (73%; kappa = 0.43; D^2 = 2.18) than of single-generation sea-ranched from wild Atlantic salmon females (60%; kappa = 0.17, D^2 = 1.04) suggest that there may also be genetic changes occurring in the former case as suggested by Fleming and Gross (1989). Once salmon have been sea ranched for several generations, allowing for the potential of genetic change and evolution in response to selection in the hatchery, divergence of adult sea-ranched from wild fish appears to be magnified.

The morphological convergence of single-generation sea-ranched and wild adults of a common genetic background is striking. The majority of environmentally induced differences in body form in cultured juveniles, particularly in head and trunk morphology, were not found in adults following natural marine rearing. This high degree of character convergence was unlikely due to effects being obscured by the mixed life-history composition of the male population (i.e., it included males that matured precociously as juveniles, as well as a small proportion that did not). Both cultured immature and mature male parr differed similarly from wild mature parr along both the first principal component and canonical discriminant function (Fig. 2), suggesting a common effect of culture. Furthermore, sea-ranched and wild females, which do not have precocial maturation, exhibited a similarly high degree of character convergence. Environmentally induced convergence in morphology is known to occur rapidly in fish when faced with similar environmental conditions (Meyer 1987; Brönmark and Miner 1992). The potential for remodelling is great in adult salmonids because they undergo considerable change in preparation for spawning, particularly in the head and trunk regions (Davidson 1935; Tchernavin 1938; Vladykov 1962). Thus, the similar genetic background, having been derived from a common genetic pool, combined with common environmental experience, including the use of the same migratory routes and exploitation of the same or very similar marine environments (Hansen and Jonsson 1991), appears to result in the major convergence seen. An alternative hypothesis that sea-ranched and wild adults have converged through selective mortality and survival of a common phenotype is unlikely because of the low overlap in morphology of cultured and wild fish as juveniles.

The proportion of a salmon's life history spent in culture is a critical determinant of divergence from its wild phenotype. Retention of fish in captivity, i.e., farming, further increases their phenotypic divergence from wild fish. Fin erosion and developmental effects appear to be reinforced or magnified during adult growth in sea pens (see also Lund et al. 1989), and new divergence occurs in body depth and adipose fin size, which increase among the adults. The increase in body depth and adipose fin size is probably due to the food-rich, low-exercise environment of sea farms relative to natural marine environments. Farmed salmon tend toward a higher fat content than wild salmon (Phillips et al. 1957; Wood et al. 1960; Aksnes et al. 1986; Bergström 1989), and the trunk is a site of fat deposition in salmonid fishes (Robinson and Mead 1973). Additionally, the food-pellet

diet may result in changes in gut and intestinal morphology that influence girth (MacLeod 1978; Weatherley and Gill 1981). The adipose fin may be a condition-dependent character (e.g., Andersson 1982; Reynolds 1993) and the degree of investment in it may reflect the physiological condition of the individual.

While there was considerable similarity in the way Imsa and Sunndalsøra farmed adults differed morphologically from wild adults, the two farmed groups also exhibited marked differences between each other. Four factors may contribute to this difference between Imsa and Sunndalsøra farmed adults. First, their unique origins may have resulted in genetic and thus morphological differences before culture (e.g., Hindar et al. 1991). The Sunndalsøra strain of salmon we studied is a mixture of several populations, while Imsa salmon are yet a different population. Thus, even under comparable farming environments the morphologies of these fish may be different. Second, differences in farming environments, while small in the present study, could produce developmental differences (e.g., Gunnes and Gjedrem 1978). Third, evolutionary divergence may have occurred due to differences in the number of generations of culture. Unintentional selection may have operated in the fifth-generation Sunndalsøra fish, but not yet in the first-generation Imsa farmed fish. Finally, the Sunndalsøra fish have been subjected to directed selection to improve "desirable" traits for aquaculture (Refstie 1990). This intense selection may again cause evolutionary changes not found in the single-generation Imsa farmed fish.

Thus, culture of salmon causes extensive environmentally induced phenotypic divergence from the wild state as a consequence of developmental influences and physical damage. Some of these phenotypic changes persist even after natural marine rearing to adulthood, as suggested by Swain et al. (1991). However, much of the phenotype converges back to the wild state. Multigeneration culture of farmed and sea-ranched salmon may result in greater divergence than that found in single-generation farmed and sea-ranched adults, suggesting that important evolutionary changes may also occur as proposed by Fleming and Gross (1989). Thus, both environmentally and genetically induced effects appear to play important roles in the phenotypic divergence of cultured salmon from their wild state.

Acknowledgements

We thank the staff of the NINA Research Station, Imsa, particularly Anders Lamberg, for their assistance during sampling, Ron Coleman and Lucy Dueck for help digitizing, and the anonymous reviewers for their comments. Financial support was provided by grants from the Norwegian Fisheries Research Council to Jonsson and Fleming and the Natural Sciences and Engineering Research Council of Canada to Gross.

References

Abbott, J.C., and L.M. Dill. 1985. Patterns of aggressive attack in juvenile steelhead trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 42: 1702–1706.

Aksnes, A., B. Gjerde, and S.O. Roald. 1986. Biological, chemical and organoleptic changes during maturation of farmed Atlantic salmon, *Salmo salar*. Aquaculture 53: 7–20.

Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. Biol. J. Linn. Soc. 17: 375–393.

Anonymous. 1992. Report of the working group on north Atlantic salmon. Int. Counc. Explor. Sea C.M. 1992/Assess:15: 155 p.

Beacham, T.D. 1990. A genetic analysis of meristic and morphometric variation in chum salmon (*Oncorhynchus keta*) at three different temperatures. Can. J. Zool. 68: 225–229.

Bergström, E. 1989. Effect of natural and artificial diets on seasonal changes in fatty acid composition and total body lipid content of wild and hatchery-reared Atlantic salmon (*Salmo salar* L.) parr–smolt. Aquaculture 82: 205–217.

Bohlin, T., C. Dellefors, and I. Faremo. 1986. Early sexual maturation of male sea trout and salmon — an evolutionary model and some practical implications. Inst. Freshwater Res. Drottningholm Rep. 63: 17–25.

Bookstein, F.L. 1990. Introduction and overview: geometry and biology, p. 61–74. *In* F.J Rohlf and F.L. Bookstein [ed.] Proceedings of the Michigan Morphometrics Workshop. Univ. Mich. Mus. Zool. Spec. Publ. No. 2: 380 p.

Brönmark, C., and J.G. Miner. 1992. Predator-induced phenotypical change in body morphology in crucian carp. Science (Wash., D.C.) 258: 1348–1350.

Currens, K.P., C.S. Sharpe, R. Hjort, C.B. Schreck, and H.W. Li. 1989. Effects of different feeding regimes on the morphometrics of chinook salmon (*Oncorhynchus tshawytscha*) and rainbow trout (*O. mykiss*). Copeia 1989: 689–695.

Davidson, F.A. 1935. The development of the secondary sexual characters in the pink salmon (*Oncorhynchus kisutch*). J. Morphol. 57: 169–183.

Dixon, W.J. [ed.] 1981. BMDP statistical software. University of California at Los Angeles Press, Los Angeles, Calif. 880 p.

Ehlinger, T.J. 1991. Allometry and analysis of morphometric variation in the bluegill, *Lepomis macrochirus*. Copeia 1991: 347–357.

Fleming, I.A. 1995. Reproductive success and the genetic threat of cultured fish to wild populations. Proceeding of the World Fisheries Congress, May 1992, Athens, Greece. Am. Fish. Soc. Symp. (In press)

Fleming, I.A., and M.R. Gross. 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution 43: 141–157.

Fleming, I.A., and M.R. Gross. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution 48: 637–657.

Gjedrem, T., H.M. Gjøen, and B. Gjerde. 1991. Genetic origin of Norwegian farmed Atlantic salmon. Aquaculture 98: 41–50.

Gjerde, B., and L.R. Schaeffer. 1989. Body traits in rainbow trout. II. Estimates of heritabilities and of phenotypic and genetic correlations. Aquaculture 80: 25–44.

Gunnes, K., and T. Gjedrem. 1978. Selection experiments with salmon. IV. Growth of Atlantic salmon during two years in the sea. Aquaculture 15: 19–33.

Hansen, L.P., and B. Jonsson. 1991. Ranching of Atlantic salmon in the River Imsa, Norway. Int. Counc. Explor. Sea C.M. 1991/M:35: 30 p.

Hansen, L.P., B. Jonsson, R.I.G. Morgan, and J.E. Thorpe. 1989. Influence of parr maturity on emigration of smolting Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 46: 410–415.

Hansen, L.P., R.A. Lund, and K. Hindar. 1987. Possible interaction between wild and reared Atlantic salmon in Norway. Int. Counc. Explor. Sea C.M. 1987/M:14: 18 p.

Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. Can. J. Fish. Aquat. Sci. 48: 945–957.

Hjort, R.C., and C.B. Schreck. 1982. Phenotypic differences among stocks of hatchery and wild coho salmon, *Oncorhynchus kisutch*, in Oregon, Washington, and California. Fish. Bull. U.S. 80: 105–119.

Hubbs, C.L., and K.F. Lagler. 1947. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor, Mich. 213 p.

Isaksson, A. 1988. Salmon ranching: a world review. Aquaculture 75: 1–33.

Johansson, N. 1981. General problems in Atlantic salmon rearing in Sweden. Ecol. Bull. (Stockholm) 34: 75–83.

Jonsson, B., and I.A. Fleming. 1993. Enhancement of wild salmon populations, p. 209–242. *In* G. Sundnes [ed.] Human impact on self-recruiting populations. An International Symposium, Kongsvoll, Norway, 7–11 June 1993. Tapir, Trondheim, Norway.

Jonsson, B., N. Jonsson, and L.P. Hansen. 1990. Does juvenile experience affect migration and spawning of adult Atlantic salmon. Behav. Ecol. Sociobiol. 26: 225–230.

Jonsson, B., N. Jonsson, and L.P. Hansen. 1991. Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. Aquaculture 98: 69–78.

Jonsson, B., and J. Ruud-Hansen. 1985. Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. Can. J. Fish. Aquat. Sci. 42: 593–595.

JONSSON, N., L.P. HANSEN, AND B. JONSSON. 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. J. Anim. Ecol. 60: 937–947.

JONSSON, N., B. JONSSON, AND L.P. HANSEN. 1988. Downstream displacement and life history traits of whitefish, *Coregonus lavaretus*, in a Norwegian river. Environ. Biol. Fishes 23: 197–204.

KLEINBAUM, D.G., AND L.L. KUPPER. 1978. Applied regression analysis and other multivariable methods. Duxbury Press, Boston, Mass. 556 p.

LEARY, R.F., F.W. ALLENDORF, AND K.L. KNUDSEN. 1985. Developmental instability as an indicator of reduced genetic variation in hatchery trout. Trans. Am. Fish. Soc. 114: 230–235.

LUND, R.A., L.P. HANSEN, AND T. JÄRVI. 1989. Identification of reared and wild salmon by external morphology, size of fins and scale characteristics. NINA Forskningsrapp. 1: 1–54. (In Norwegian with English summary)

MACLEOD, M.G. 1978. Effects of salinity and starvation on the alimentary canal anatomy of the rainbow trout *Salmo gairdneri* Richardson. J. Fish Biol. 12: 71–79.

MARTIN, W.R. 1949. The mechanics of environmental control of body form in fishes. Univ. Toronto Stud. Biol. Ser. 58. Publ. Ont. Fish. Res. Lab. 70: 1–72.

MEYER, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. Evolution 41: 1357–1369.

MORING, J.R. 1982. Fin erosion and culture-related injuries in chinook salmon raised in floating net pens. Prog. Fish-Cult. 44: 189–191.

NOVOTNY, A.J. 1980. Delayed release of salmon, p. 325–369. *In* J.E. Thorpe [ed.] Salmon ranching. Academic Press, New York, N.Y. 441 p.

PHILLIPS, A.M. JR., D.R. BROCKWAY, F.E. LOVELACE, AND H.A. PODOLIAK. 1957. A chemical comparison of hatchery and wild brook trout. Prog. Fish-Cult. 21: 3–16.

PIMENTEL, R.A. 1979. Morphometrics: the multivariate analysis of biological data. Kendall/Hunt, Dubuque, Iowa.

REISENBICHLER, R.R., AND J.D. MCINTYRE. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 34: 123–128.

REFSTIE, T. 1990. Application of breeding schemes. Aquaculture 85: 163–169.

REIST, J.D. 1986. An empirical evaluation of coefficients used in residual and allometric adjustment of size covariation. Can. J. Zool. 64: 1363–1368.

REYNOLDS, J.D. 1993. Should attractive individuals court more? Theory and a test. Am. Nat. 141: 914–927.

RICE, W.R. 1989. Analysing tables of statistical tests. Evolution 43: 223–225.

RIDDELL, B.E., W.C. LEGGETT, AND R.L. SAUNDERS. 1981. Evidence of adaptive polygenic variation between two populations of Atlantic salmon (*Salmo salar*) native to tributaries of the S.W. Miramichi River, N.B. Can. J. Fish. Aquat. Sci. 38: 321–333.

ROBINSON, J.S., AND J.F. MEAD. 1973. Lipid absorption and deposition in rainbow trout (*Salmo gairdneri*). Can. J. Biochem. 51: 1050–1058.

ROHLF, J.F., AND F.L. BOOKSTEIN. 1987. A comment on shearing as a method for "size correction". Syst. Zool. 36: 356–367.

ROHLF, J.F., AND F.L. BOOKSTEIN [ED.] 1990. Proceedings of the Michigan Morphometrics Workshop. Univ. Mich. Mus. Zool. Spec. Publ. No. 2: 380 p.

SODERBERG, R.W., AND J.W. MEADE. 1987. Effects of rearing density on growth, survival, and fin condition of Atlantic salmon. Prog. Fish-Cult. 49: 280–283.

STRAUSS, R.E., AND F.L. BOOKSTEIN. 1982. The truss: body form reconstruction in morphometrics. Syst. Zool. 31: 113–135.

SWAIN, D.P., AND B.E. RIDDELL. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. 47: 566–571.

SWAIN, D.P., B.E. RIDDELL, AND C.B. MURRAY. 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*): environmental versus genetic origin. Can. J. Fish. Aquat. Sci. 48: 1783–1791.

TAYLOR, E.B. 1986. Differences in morphology between wild and hatchery populations of juvenile coho salmon. Prog. Fish-Cult. 48: 171–176.

TAYLOR, E.B., AND J.D. MCPHAIL. 1985. Variation in body morphology among British Columbia populations of coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 42: 2020–2028.

TCHERNAVIN, V. 1938. Changes in the salmon skull. Trans. Zool. Soc. Lond. 24: 104–184.

THORPE, R.S. 1983. A review of the numerical methods for recognising and analysing racial differentiation, p. 404–423. *In* J. Felsenstein [ed.] Numerical taxonomy. Springer-Verlag, Berlin.

TITUS, K., J.A. MOSHER, AND B.K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. Am. Midl. Nat. 11: 1–7.

VLADYKOV, V.D. 1962. Osteological studies of Pacific salmon of the genus *Oncorhynchus*. Bull. Fish. Res. Board Can. 136: 172 p.

WAPLES, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Can. J. Fish. Aquat. Sci. 48(Suppl. 1): 124–133.

WEATHERLEY, A.H., AND H.S. GILL. 1981. Recovery growth following periods of restricted rations and starvation in rainbow trout *Salmo gairdneri* Richardson. J. Fish Biol. 18: 195–208.

WINANS, G.A. 1984. Multivariate morphometric variability in Pacific salmon: technical demonstration. Can. J. Fish. Aquat. Sci. 41: 1150–1159.

WOOD, E.M., W.T. YASUTAKE, J.E. HALVER, AND A.N. WOODALL. 1960. Chemical and histological studies of wild and hatchery salmon in fresh water. Trans. Am. Fish. Soc. 89: 301–307.

Appendices

APPENDIX 1. Mean morphological measurements (distances in mm and areas in mm^2) and ANOVA of cultured and wild parr Atlantic salmon. Measurements are adjusted to the mean centroid size of all the parr examined (192 438 mm^2, which approximates a body weight of 31.34 g). Character numbers in parentheses refer to landmark locations (Fig. 1). All significantly different groups based on pairwise comparison (Scheffé's method; $P < 0.05$) are given in parentheses below each character measurement. Only measurements differing significantly among fish groups by sequential Bonferroni tests are shown.

Region and Character	Cultured			Wild	ANOVA	
	Female	Male		male		
	Immature (C_{fi})	Immature (C_{mi})	Mature (C_{mm})	mature (W_{mm})	$F_{3,63}$	P
Fins						
Pectoral fin length (13–14)	23.39 (C_{mm}, W_{mm})	23.28 (C_{mm}, W_{mm})	24.30 (C_{fi}, C_{mi}, W_{mm})	28.67 (C_{fi}, C_{mi}, C_{mm})	140.46	<0.001
Pelvic fin length (5–17)	15.70 (W_{mm})	15.64 (W_{mm})	15.64 (W_{mm})	17.43 (C_{fi}, C_{mi}, C_{mm})	11.62	<0.001
Dorsal fin height (6–16)	20.24	19.92	18.12 (W_{mm})	20.76 (C_{mm})	4.96	0.004
Anal fin height (7–18)	15.25 (W_{mm})	14.79 (W_{mm})	15.13 (W_{mm})	17.12 (C_{fi}, C_{mi}, C_{mm})	14.42	<0.001
Anal fin base (7–9)	9.94 (W_{mm})	10.03 (W_{mm})	10.59	11.35 (C_{fi}, C_{mi})	7.97	<0.001
Caudal fin area	428.39 (W_{mm})	430.23 (W_{mm})	451.15 (W_{mm})	523.06 (C_{fi}, C_{mi}, C_{mm})	38.43	<0.001
Head						
Snout length (2–19)	8.20 (C_{mm}, W_{mm})	8.32 (C_{mm}, W_{mm})	9.38 (C_{fi}, C_{mi})	9.82 (C_{fi}, C_{mi})	18.54	<0.001
Snout to below premaxilla (truss 1–2)	11.28 (C_{mm}, W_{mm})	11.31 (C_{mm}, W_{mm})	12.67 (C_{fi}, C_{mi}, W_{mm})	13.63 (C_{fi} , C_{mi}, C_{mm})	58.51	<0.001
Snout to below pectoral (truss 2–3)	26.24 (C_{mm}, W_{mm})	26.36 (W_{mm})	27.05 (C_{fi}, W_{mm})	28.94 (C_{fi}, C_{mi}, C_{mm})	41.11	<0.001
Forehead length (truss 2–4)	23.45 (C_{mm}, W_{mm})	23.50 (C_{mm}, W_{mm})	25.67 (C_{fi}, C_{mi})	26.76 (C_{fi}, C_{mi})	27.35	<0.001
Head depth 1 (truss 1–4)	21.12 (C_{mm}, W_{mm})	21.00 (C_{mm}, W_{mm})	22.88 (C_{fi}, C_{mi})	23.45 (C_{fi}, C_{mi})	21.02	<0.001
Head depth 2 (truss 3–4)	21.19 (C_{mm}, W_{mm})	20.77 (C_{mm}, W_{mm})	22.35 (C_{fi}, C_{mi}, W_{mm})	23.37 (C_{fi}, C_{mi}, C_{mm})	36.58	<0.001
Anterior trunk						
Body depth (6–15)	28.33 (C_{mm}, W_{mm})	28.06 (C_{mm}, W_{mm})	29.62 (C_{fi}, C_{mi})	30.13 (C_{fi}, C_{mi})	11.91	<0.001
Below pectoral to pelvic fin (truss 3–5)	43.39	43.28	44.20 (W_{mm})	42.38 (C_{mm})	5.02	0.004
Below pectoral to dorsal fin (truss 3–6)	39.77 (W_{mm})	39.42 (W_{mm})	40.37 (W_{mm})	42.11 (C_{fi}, C_{mi}, C_{mm})	19.38	<0.001
Head to dorsal fin (truss 4–6)	33.80 (W_{mm})	33.58 (W_{mm})	32.91 (W_{mm})	35.33 (C_{fi}, C_{mi}, C_{mm})	7.86	<0.001
Posterior trunk						
Dorsal to anal fin (truss 6–7)	45.33 (W_{mm})	45.43 (W_{mm})	45.60 (W_{mm})	43.86 (C_{fi}, C_{mi}, C_{mm})	10.45	<0.001
Dorsal to qdipose fin (truss 6–10)	45.57 (W_{mm})	46.03 (W_{mm})	45.61 (W_{mm})	43.43 (C_{fi}, C_{mi}, C_{mm})	9.91	<0.001
Anal to qdipose fin (truss 7–10)	20.57 (C_{mm})	20.53 (C_{mm})	21.42 (C_{fi}, C_{mi})	21.01	5.99	0.001
Tail						
Caudal peduncle depth (truss 11–12)	10.49 (C_{mm}, W_{mm})	10.34 (C_{mm}, W_{mm})	11.09 (C_{fi}, C_{mi}, W_{mm})	11.70 (C_{fi}, C_{mi}, C_{mm})	42.87	<0.001

APPENDIX 2. Mean morphological measurements (distances in cm and areas in cm^2) and ANOVA of wild, sea-ranched, and farmed female adult Atlantic salmon. Females photographed in 1989, including all farmed Imsa females, could not be measured for some characters. Measurements are adjusted to the mean size of the females in the comparison (full female sample: 65.36 cm fork length; reduced female sample: 46 837 cm^2 centroid size, which approximates 66.36 cm fork length). Character numbers in parentheses refer to landmark locations (Fig. 1). Year effects and year-by-fish group interactions were included in the analyses and where significant mean morphological measurements are adjusted to a constant year. All significantly different groups based on pairwise comparison (Scheffé's method; $P < 0.05$) are given in parentheses below each character measurement. Only measurements differing significantly among fish groups by sequential Bonferroni tests are shown (full female sample: df = 3,135; reduced female sample: df = 2,109).

Region and character	River Imsa			Sunndalsøra farmed (F_s)	ANOVA	
	Wild (W_i)	Sea ranched (SR_i)	Farmed (F_i)		*F*	*P*
Fins						
Pectoral fin length (13–14)	8.15 (F_i, F_s)	8.01 (F_i, F_s)	7.57 (W_i, SR_i, F_s)	6.80 (W_i, SR_i, F_i)	52.04	<0.001
Pelvic fin length (5–17)	6.19 (F_i, F_s)	6.30 (F_i, F_s)	6.01 (W_i, SR_i, F_s)	5.17 (W_i, SR_i, F_i)	32.82	<0.001
Dorsal fin height (6–16)	7.63 (SR_i, F_i, F_s)	7.02 (W_i, F_i, F_s)	4.99 (W_i, SR_i)	4.97 (W_i, SR_i)	38.37	<0.001
Dorsal fin base (6–8)	7.30	7.16 (F_s)	7.24	7.56 (SR_i)	4.88	0.003
Anal fin height (7–18)	6.79 (F_s)	6.72 (F_s)	6.71 (F_s)	6.04 (W_i, SR_i, F_i)	21.76	<0.001
Adipose fin area	3.18 (F_i, F_s)	3.40 (F_i, F_s)	5.14 (W_i, SR_i)	5.12 (W_i, SR_i)	29.55	<0.001
Caudal fin area	104.65 (F_i, F_s)	105.46 (F_i, F_s)	94.10 (W_i, SR_i)	88.38 (W_i, SR_i)	68.72	<0.001
Head						
Snout length (2–19)	3.88 (F_i)	3.94 (F_i)	4.84 (W_i, SR_i)	4.00	4.88	0.003
Lower jaw length (20–22)	2.89 (F_i, F_s)	2.79 (F_i, F_s)	3.79 (W_i, SR_i)	3.20 (W_i, SR_i)	16.03	<0.001
Kype height (21–23)	1.38 (F_s)	1.33 (F_s)	1.45 (F_s)	0.95 (W_i, SR_i, F_i)	27.49	<0.001
Snout to below premaxilla (truss 1–2)	6.33 (F_i, F_s)	6.17 (F_i, F_s)	7.30 (W_i, SR_i, F_s)	6.86 (W_i, SR_i, F_i)	37.44	<0.001
Snout to below pectoral (truss 2–3)	12.94 (F_s)	12.94 (F_s)		13.26 (W_i, SR_i)	5.96	0.003
Forehead length (truss 2–4)	10.18 (F_i)	10.26 (F_i)	11.54 (W_i, SR_i, F_s)	10.56 (F_i)	17.12	<0.001
Head depth 1 (truss 1–4)	9.66 (F_s)	9.58 (F_i, F_s)	10.07 (SR_i, F_s)	10.59 (W_i, SR_i, F_i)	17.01	<0.001
Head depth 2 (truss 3–4)	10.02 (F_s)	10.11 (F_s)		11.05 (W_i, SR_i)	85.54	<0.001
Anterior trunk						
Body depth (6–15)	12.51 (F_s)	12.68 (F_s)		14.54 (W_i, SR_i)	48.85	<0.001
Below pectoral to pelvic fin (truss 3–5)	20.83 (SR_i, F_s)	21.19 (W_i, F_s)		21.61 (W_i, SR_i)	16.31	<0.001
Below pectoral to dorsal fin (truss 3–6)	19.58 (F_s)	19.73 (F_s)		20.96 (W_i, SR_i)	19.81	<0.001
Head to pelvic fin (truss 4–5)	24.84 (F_s)	25.02		25.23 (W_i)	8.63	<0.001
Head to dorsal fin (truss 4–6)	17.66 (F_i, F_s)	17.37 (F_i)	16.47 (W_i, SR_i)	16.99 (W_i)	7.83	<0.001
Pelvic to dorsal fin (truss 5-6)	12.43 (F_s)	12.84 (F_s)		14.63 (W_i, SR_i)	63.39	<0.001
Posterior trunk						
Pelvic to anal fin (truss 5–7)	13.50 (SR_i, F_s)	13.10 (W_i, F_s)		12.79 (W_i, SR_i)	17.05	<0.001
Pelvic to adipose fin (truss 5–10)	19.87 (SR_i)	19.36 (W_i, F_s)		19.83 (SR_i)	9.13	<0.001
Dorsal to anal fin (truss 6–7)	21.42 (F_s)	21.43 (F_s)		21.93 (W_i, SR_i)	10.38	<0.001

APPENDIX 2. (*Concluded*)

Region and character	River Imsa			Sunndalsøra farmed (F_s)	ANOVA	
	Wild (W_i)	Sea ranched (SR_i)	Farmed (F_i)		*F*	*P*
Dorsal to adipose fin (truss 6–10)	22.11 (F_i, F_s)	21.71 (F_i)	20.73 (W_i, SR_i, F_s)	21.46 (W_i, F_i)	10.93	<0.001
Anal to adipose fin (truss 7–10)	9.92 (F_s)	9.72 (F_s)		10.64 (W_i, SR_i)	28.32	<0.001
Tail						
Anal to caudal fin, dorsal (truss 7–12)	14.11 (F_s)	14.19 (F_s)		14.89 (W_i, SR_i)	16.78	<0.001
Adipose to caudal fin, ventral (truss 10–11)	9.48 (F_i, F_s)	9.56 (F_i, F_s)	9.97 (W_i, SR_i)	10.00 (W_i, SR_i)	11.57	<0.001
Adipose to caudal fin, dorsal (10–12)	7.98 (F_i, F_s)	8.15 (F_i, F_s)	8.58 (W_i, SR_i)	8.60 (W_i, SR_i)	10.32	<0.001
Caudal peduncle depth (truss 11-12)	4.86 (F_i, F_s)	4.83 (F_i, F_s)	5.33 (W_i, SR_i)	5.20 (W_i, SR_i)	33.26	<0.001

APPENDIX 3. Mean morphological measurements (distances in cm and areas in cm^2) and ANOVA of wild, sea-ranched, and farmed male adult Atlantic salmon. Males photographed in 1989, including all farmed Imsa males, could not be measured for some characters. Measurements are adjusted to the mean size of the males in the comparison (full male sample: 60.94 cm fork length; reduced male sample: 37 132 cm^2 centroid size, which approximates 60.79 cm fork length). Character numbers in parentheses refer to landmark locations (Fig. 1). Year effects and year-by-fish group interactions were included in analyses and where significant mean morphological measurements are adjusted to a constant year. All significantly different groups based on pairwise comparison (Scheffé's method; $P < 0.05$) are given in parentheses below each character measurement. Only measurements differing significantly among fish groups by sequential Bonferroni tests are shown (full male sample: df = 3,143; reduced male sample: df = 2,116).

Region and character	River Imsa			Sunndalsøra farmed (F_s)	ANOVA	
	Wild (W_i)	Sea ranched (SR_i)	Farmed (F_i)		*F*	*P*
Fins						
Pectoral fin length (13–14)	8.02 (SR_i, F_i, F_s)	7.71 (W_i, F_s)	7.58 (W_i, F_s)	6.94 (W_i, SR_i, F_i)	23.20	<0.001
Pelvic fin length (5–17)	6.03 (F_i, F_s)	6.02 (F_i, F_s)	5.55 (W_i, SR_i)	5.66 (W_i, SR_i)	4.69	0.004
Dorsal fin height (6–16)	7.05 (SR_i, F_i, F_s)	6.33 (W_i, F_i, F_s)	5.11 (W_i, SR_i)	5.18 (W_i, SR_i)	24.86	<0.001
Dorsal fin base (6–8)	6.77 (SR_i)	6.40 (W_i, F_i, F_s)	6.75 (SR_i)	7.00 (SR_i)	15.39	<0.001
Anal fin height (7–18)	6.58 (F_i, F_s)	6.38 (F_i)	5.96 (W_i, SR_i, F_s)	6.21 (W_i, F_i)	7.62	<0.001
Adipose fin area	4.93 (F_i, F_s)	4.73 (F_i, F_s)	6.37 (W_i, SR_i)	5.96 (W_i, SR_i)	7.80	<0.001
Caudal fin area	92.64 (SR_i, F_i, F_s)	90.41 (W_i, F_i, F_s)	83.59 (W_i, SR_i)	82.71 (W_i, SR_i)	31.05	<0.001
Head						
Lower jaw length (20–22)	4.32 (F_i)	4.23 (F_i)	5.16 (W_i, SR_i, F_s)	4.56 (F_i)	9.78	<0.001
Kype height (21–23)	2.18 (F_s)	2.11 (F_s)	2.14 (F_s)	1.71 (W_i, SR_i, F_i)	24.95	<0.001
Snout to below premaxilla (truss 1–2)	7.74 (F_i, F_s)	7.58 (F_i, F_s)	8.37 (W_i, SR_i)	8.16 (W_i, SR_i)	7.86	<0.001
Snout to below pectoral (truss 2–3)	13.96 (F_s)	13.86 (F_s)		14.64 (W_i, SR_i)	13.13	<0.001
Head depth 1 (truss 1–4)	9.60 (SR_i, F_s)	9.41 (W_i, F_s)	9.65 (F_s)	10.65 (W_i, SR_i, F_i)	30.05	<0.001
Head depth 2 (truss 3–4)	9.39 (F_s)	9.33 (F_s)		10.22 (W_i, SR_i)	54.41	<0.001
Anterior trunk body depth (6–15)	10.96 (F_s)	11.09 (F_s)		12.19 (W_i, SR_i)	25.49	<0.001

APPENDIX 3. (*Concluded*)

Region and character	River Imsa			Sunndalsøra farmed (F_s)	ANOVA	
	Wild (W_i)	Sea ranched (SR_i)	Farmed (F_i)		*F*	*P*
Head to dorsal fin (truss 4–6)	15.85 (F_i, F_s)	15.78 (F_i, F_s)	14.75 (W_i, SR_i)	14.79 (W_i, SR_i)	22.04	<0.001
Pelvic to dorsal fin (truss 5–6)	11.47 (F_s)	11.52 (F_s)		12.76 (W_i, SR_i)	39.46	<0.001
Posterior trunk						
Pelvic to anal fin (truss 5–7)	11.63 (F_s)	11.53 (F_s)		11.11 (W_i, SR_i)	11.75	<0.001
Pelvic to adipose fin (truss 5–10)	17.59 (F_s)	17.36		17.30 (W_i)	9.22	0.001
Dorsal to anal fin (truss 6–7)	18.78 (F_s)	18.82 (F_s)		19.63 (W_i, SR_i)	33.90	<0.001
Dorsal to adipose fin (truss 6–10)	19.49 (F_i)	19.13 (F_i)	18.51 (W_i, SR_i, F_s)	19.32 (F_i)	6.09	0.001
Anal to adipose fin truss 7–10)	9.16 (F_s)	9.19 (F_s)		9.71 (W_i, SR_i)	10.96	<0.001
Tail						
Anal to zaudal fin, ventral (truss 7–11)	10.48 (F_s)	10.34 (F_s)		10.78 (W_i, SR_i)	7.29	0.001
Anal to caudal fin, dorsal (truss 7–12)	12.80 (F_s)	12.74 (F_s)		13.29 (W_i, SR_i)	8.26	<0.001
Adipose to caudal fin, ventral (truss 10–11)	8.98 (F_s)	9.01 (F_s)	8.90 (F_s)	9.29 (W_i, SR_i, F_i)	4.96	0.003

Patterns in Algal Recruitment from Sediment to Water in a Dimictic, Eutrophic Lake

Lars-Anders Hansson

Institute of Ecology/Limnology, Ecology Building, S-22362 Lund, Sweden

Lars G. Rudstam

Cornell Biological Field Station and Department of Natural Resources, Cornell University, 900 Shackelton Point Road, Bridgeport, NY 13030-9750, USA

Timothy B. Johnson and Patricia Soranno

Center for Limnology, University of Wisconsin, 680 N. Park Street, Madison, WI 53706, USA

and Yvonne Allen

Ontario Ministry of Natural Resources, Fisheries Research, P.O. Box 5000, Maple, ON L6A 1S9, Canada

Hansson, L.-A., L.G. Rudstam, T.B. Johnson, P. Soranno, and Y. Allen. 1994. Patterns in algal recruitment from sediment to water in a dimictic, eutrophic lake. Can. J. Fish. Aquat. Sci. 51: 2825–2833.

In the large, dimictic, and highly productive Lake Mendota (Wisconsin, USA), the recruitment rates from sediment to water were determined for some characteristic and dominating algal species during a 1-yr cycle. Quantifying recruitment in relation to abundance in the water on a whole-lake basis revealed that recruitment usually accounted for less than 1% of the total standing stock of each species per day, indicating that recruitment may not be an important population variable in Lake Mendota, but may instead function as an inoculum for future growth in the water column. The recruitment of *Cryptomonas erosa* and *Ceratium hirundinella* showed a dephasing among sites, suggesting that algae on the sediment surface rise into the water column in response to some depth-related cue. With the exception of one recruitment period for *Aphanizomenon*, no recruitment was recorded below the thermocline during the stratification period, indicating that a variable associated with stratified conditions affected algal movements from the hypolimnion to the euphotic zone. We argue that the understanding of recruitment patterns from sediment to water is a key factor in managing algal blooms in highly productive lakes.

Dans le lac Mendota (Wisconsin, É.-U.), un grand lac dimictique très productif, on a déterminé les taux de recrutement dans la colonne d'eau de certaines espèces d'algues caractéristiques et dominantes en provenance des sédiments au cours d'un cycle annuel. La quantification du recrutement en rapport avec l'abondance des algues dans l'eau dans l'ensemble du lac a montré que le recrutement ne fournit habituellement que moins de 1 % de la quantité totale d'algues de chaque espèce par jour, ce qui indique que le recrutement ne serait pas une variable importante des populations d'algues dans le lac Mendota; il pourrait plutôt agir comme un processus d'inoculation assurant la croissance future des algues dans la colonne d'eau. On a observé un déphasage spatial entre les recrutements de *Cryptomonas erosa* et *Ceratium hirundinella*, ce qui laisse penser que les algues présentent à la surface des sédiments s'élèvent dans la colonne d'eau en fonction d'un signal lié à la profondeur. À l'exception d'une période de recrutement d'*Aphanizomenon*, le recrutement était nul sous la thermocline durant la période de stratification, ce qui indique qu'un facteur lié aux conditions de stratification a entravé le passage des algues de l'hypolimnion à la zone euphotique. La compréhension des processus de recrutement des algues dans la colonne d'eau à partir des sédiments est de toute première importance pour la gestion des proliférations d'algues dans les lacs très productifs.

Received July 20, 1993
Accepted May 30, 1994
(J12018)

Reçu le 20 juillet 1993
Accepté le 30 mai 1994

Algal migration within the water column is a phenomenon that has been discussed in the scientific literature for decades (Lund 1954) and has been described for various algal groups, including flagellated species (Cullen and Horrigan 1981), and cyanophytes (=cyanobacteria) (Reynolds 1972). Although the physiological structures responsible for migration, such as flagella and vacuoles, have been evaluated in detail (Reynolds 1972; Walsby and Klemer 1974; Kromkamp et al. 1988), surprisingly few studies have focused on the ecological consequences of the differences in migratory behaviour among different algal species. An obvious advantage of being motile is that such cells can remain in the euphotic zone, which is especially important in highly productive lakes where light attenuation is rapid (Konopka et al. 1978). Another advantage on a longer time scale is that cells or colonies may be recruited from the sediment surface when conditions become favourable in the water column and vice versa. One habitat may be used as an inoculum

for rapid colonization of the other. The cyanophyte *Microcystis* is known to form dense vegetative mats on the sediment surface during fall and winter (Fallon and Brock 1981), and *Ceratium hirundinella*, for example, regularly forms cysts on the sediment surface (Heaney et al. 1983). The use of and the shift between different habitats, in this case the water column and the sediment surface, opens up intriguing aspects of algal ecology.

Frequent blooms of different cyanophytic species often cause severe problems in highly productive lakes. Blooms appear rapidly (within hours; Reynolds and Walsby 1975), implying that not only growth but also other factors such as migration to surface waters may be involved (Klemer 1976; Konopka et al. 1978; Klemer and Konopka 1989). Several recent studies have suggested that migration of blue-green algae may be a considerable factor behind internal nutrient loading in eutrophic lakes (Osgood 1988; Barbiero and Welch 1992; Pettersson et al. 1992; Barbiero 1993). Hence, knowledge of algal recruitment patterns and of the factors initiating recruitment from the sediment surface is necessary for understanding bloom formation in productive lakes and developing tools to manage such blooms. Moreover, migratory behaviour may have an impact on dynamics in the algal community and may partly explain rapid alterations in dominance and succession patterns (Hansson 1993).

Our aim in this study was to measure changes in environmental variables (nutrient and oxygen concentrations, temperature and light regimes, wind speed, and water column stability) simultaneously with recruitment and sinking patterns of selected algal species during a 1-yr cycle. Among the many species that performed regular migrations in the lake we investigated (Lake Mendota, Wisconsin, USA), four (*Aphanizomenon flos-aquae*, *Microcystis aeruginosa*, *Cryptomonas erosa*, and *Ceratium hirundinella*) were selected and studied in detail because (1) they showed migratory behaviour, (2) they were common in the lake, (3) they are commonly found in highly productive lakes, and (4) these four species represent different life strategies and morphologies (e.g., they differ in size, have gas vacuoles or flagella, and are vegetative or form cysts) that should lead to differences in migratory behaviour.

Material and Methods

Lake Mendota is a dimictic, hardwater lake situated in southcentral Wisconsin, USA, with a surface area of 39.1 km^2, a maximum depth of 25 m, and a mean depth of 12.4 m. The lake has a long history of limnological studies (Birge and Juday 1922; Fallon and Brock 1980; Brock 1985; Kitchell 1992).

In our study, recruitment and sinking patterns of four algal species were studied in detail, including *C. erosa*, *C. hirundinella*, *M. aeruginosa*, and *A. flos-aquae*. *Cryptomonas erosa* is small compared with the other three species (greatest axial linear dimension (GALD) 18 μm; biovolume 504 μm3) and probably highly vulnerable to grazing, suggesting that the abundance of grazers may affect recruitment patterns and abundance in the water column. *Ceratium hirundinella* is large (GALD 193 μm; biovolume 44 000 μm^3), with large spines protecting it from grazing, suggesting that grazer abundance may not affect this species. Furthermore, *Ceratium* has a complicated life cycle including cyst formation in the sediments (Heaney et al. 1983). The blue-green alga *M. aeruginosa* (GALD per colony 40 μm; biovolume 4074 μm^3) is a colonial form with a mucus cover, probably reducing its vulnerability to grazing. Finally, *A. flos-aquae* is a filamentous alga (GALD per filament 115 μm; biovolume 709 μm^3) able to form macroscopic bundles.

Traps to measure recruitment and sinking of algae were made of glass jars filled with filtered lake water (i.e., no algae present in the trap at the start) with a funnel through the lid. A 300-μm-mesh net covered the entrance of the funnel to reduce grazing by zooplankters on trapped algae. We sampled 16 times from January to December 1991, and each trapping period lasted 48 h. On each sampling occasion, two funnel traps (one with the funnel facing up, the other down, catching downward and upward migrations, respectively) were attached to an aluminium cube frame (Fig. 1), fixing the trap entrances at 0.75 m from the sediment surface. This depth was chosen to avoid disturbance of the soft sediment surface, including the algal community, which would have been the case if traps had been put direcly on the sediment surface. On each sampling occasion, three cube frames were set at 2, 7, and 23 m water depth, respectively. After 48 h, the traps were recovered and trapped algae were preserved in Lugol solution. Subsamples were filtered on 0.45-μm membrane filters (GN-6; Gelman) and permanently mounted on slides with HPMA (2-hydroxypropyl metacrylate; Crumpton 1987), prior to counting and identification.

A potential problem with this trapping method is the influence of horizontal, current-driven, transport of algal cells below the recruitment traps (0–0.75 m from the sediment surface). Since traps are covered with 300-μm-mesh net and the current velocity is lower inside the trap than outside, this artefact is unlikely to have affected the recorded recruitment rates. Moreover, when Hansson (1993) put traps inside plastic enclosures, where current velocities were at a minimum, recruitment rates were in the same order of magnitude as in the present study.

Samples for routine limnological analysis, including temperature profiles, dissolved oxygen, nutrients, transparency, and phytoplankton and zooplankton abundances, were collected at either weekly or biweekly intervals throughout the open-water season. During winter, samples were taken monthly through the ice at a deep hole in the middle of the lake. Samples were always collected during the same week as recruitment and sinking of algae were quantified. Temperature and oxygen measurements were done at 1-m intervals with a calibrated YSI thermistor and oxygen probe. Light profiles were measured with a Li-Cor quantum meter (micromoles quanta per square metre per second) and expressed as extinction coefficient (light attenuation per metre). For days when the extinction coefficients were not determined, Secchi depth measurements were transformed to extinction coefficients using the relationship

$$\text{Extinction coefficient} = 1.11/\text{Secchi depth} + 0.25 \quad (n = 30;\ r = 0.84).$$

Zooplankton were collected with vertical tows using a plankton net (diameter 0.70 m; mesh size 130 μm). The animals were counted and measured in the laboratory under a dissecting microscope. Phytoplankton were collected from an unfiltered integrated tube sample (inner diameter 21 mm) from 0 to 8 m (epilimnion) and preserved in glutaraldehyde. Phytoplankton were identified and counted from permanent slides (St. Amand; Phycotech Inc.) for all dates associated

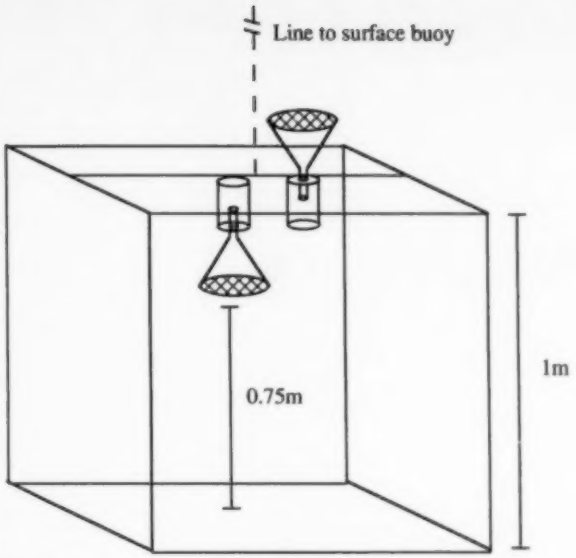


FIG. 1. Equipment used to trap algae migrating to and from the sediment surface, consisting of an aluminium cube frame (1 m^3), with one funnel-trap facing downwards trapping upward migration, and one facing upwards, trapping downward migration. The funnel gaps were covered with 300-μm-mesh nylon nets, excluding the major part of the zooplankton from the traps.

with trap data. Water for analysis of dissolved reactive and total phosphorus was taken from the integrated tube sample. Water column stability was calculated from the temperature profiles and expressed as Schmidt stability (Schmidt 1928). This number depends on density differences in the water column and is high when the temperature gradient between the epi- and hypolimnion is large and estimates the amount of work required to mix the lake to uniform density without adding or subtracting heat. Mixed conditions give a Schmidt stability number close to zero. Additional details on the routine sampling program are described in Kitchell (1992). Data on wind speed was collected daily at the Dane County regional airport, Madison, Wis., by the National Climatic Data Center.

Results

Lake Mendota was stratified with respect to temperature between 20 May and 23 September and completely mixed between 1 January and 7 May, and 7 October and 31 December (Fig. 2). The periods between 7 and 20 May, and 23 September and 7 October may be regarded as transitional periods between stratified and mixed conditions. The strength of the stratification is also expressed by the water column stability (Schmidt's number), which was close to zero (indicating mixed conditions) from the beginning of the year to 2 May (Fig. 2). Thereafter, values rapidly increased to a stable maximum that lasted until 21 September. In October, water column stability values again decreased to low values similar to those seen in the spring (Fig. 2). With respect to dissolved oxygen, Lake Mendota was stratified from the first sampling occasion (29 January) until ice-out (24 March). From ice-out until 20 May, the oxygen concentration

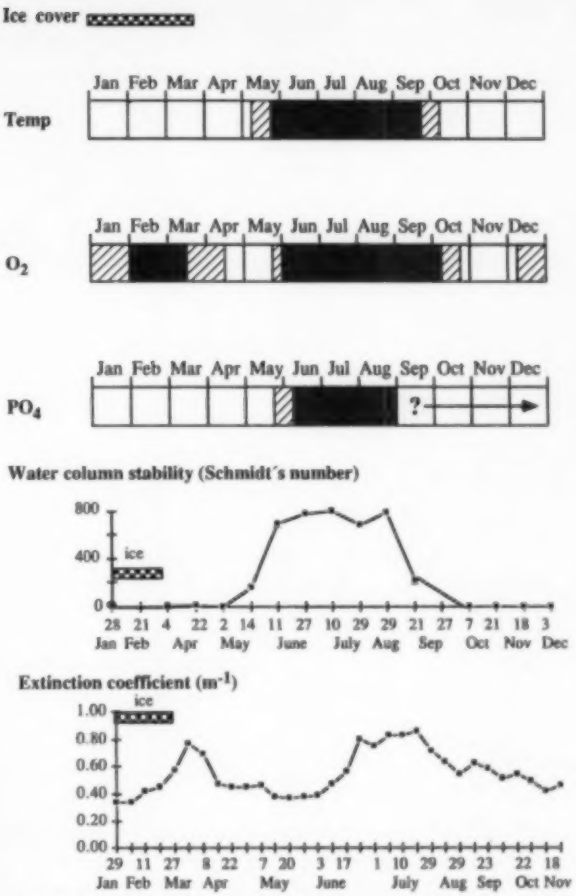

Ice cover
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Temp
O2
PO4
?
Water column stability (Schmidt's number)
800
400
0
ice
28 21 4 22 2 14 11 27 10 29 29 21 27 7 21 18 3
Jan Feb Apr May June July Aug Sep Oct Nov Dec
Extinction coefficient (m-1)
1.00
0.80
0.60
0.40
0.20
0.00
29 11 27 8 22 7 20 3 17 1 10 29 29 23 22 18
Jan Feb Mar Apr May June July Aug Sep Oct Nov

FIG. 2. Periods when Lake Mendota was stratified (black) with respect to temperature, dissolved oxygen, and dissolved phosphate phosphorus (PO_4-P) from 1 January to 31 December 1991. White areas indicate complete mixing of the variable (i.e., the concentration of the variable was equal throughout the water column). Hatched areas indicate transitional periods between mixing and stratification. Water column stability and light extinction coefficients as well as periods with ice cover are also given.

was similar throughout the entire water column. Between 31 May and 7 October the oxygen concentration in bottom water (23 m) was usually zero, and always below 4 $mg \cdot L^{-1}$. A few weeks after the fall turnover in mid-October, oxygen-rich water had reached the sediment surface at 23 m (Fig. 2). A summer stratification in dissolved reactive phosphorus (PO_4-P) developed simultaneously with oxygen stratification (Fig. 2).

The light extinction coefficient varied between 0.34 and 0.88 $\cdot m^{-1}$ during the year (Fig. 2), with one maximum (high light attenuation) in the beginning of April and one from late June to late July. Between these maxima, the extinction coefficient was usually below 0.5 $\cdot m^{-1}$ (Fig. 2).

Zooplankton were divided into three groups: large (*Daphnia galeata* and *Daphnia pulicaria*; mean lengths 1.46 and 1.49 mm, respectively); small: calanoid and cyclopoid copepods (mean lengths 0.66 and 0.67 mm, respectively), and Rotifers (length <0.50 mm). The abundance of zooplankton

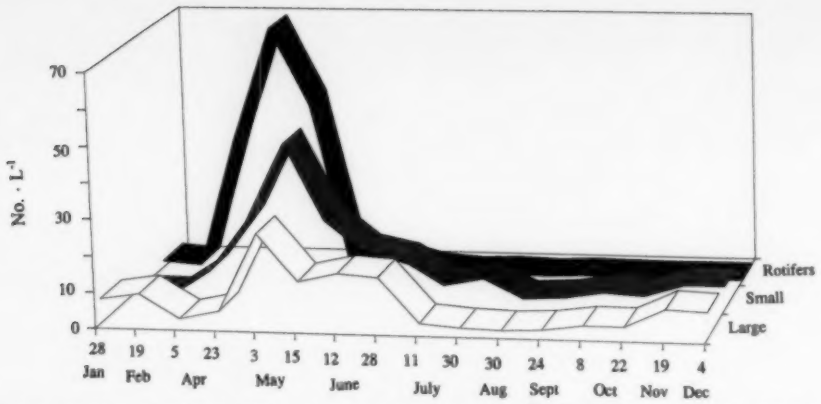


FIG. 3. Abundance of large (*D. galeata* and *D. pulicaria*) and small copepods and rotifers in Lake Mendota during 1991.

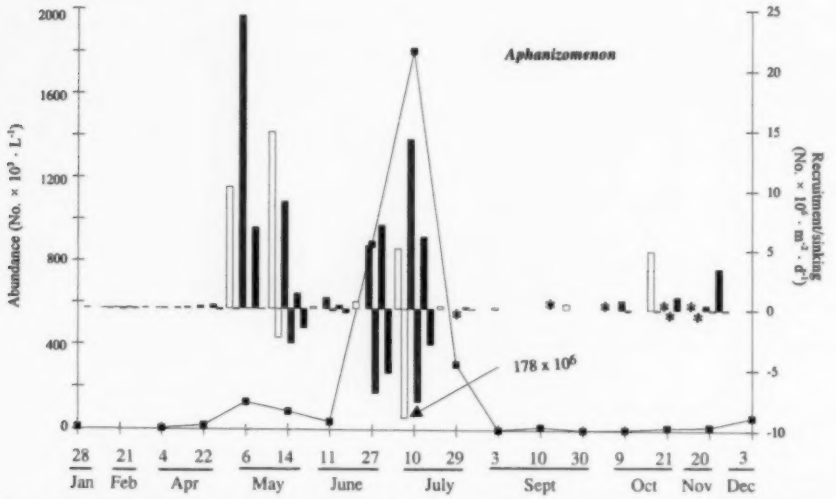


FIG. 4. Population dynamics of *A. flos-aquae* in Lake Mendota during 1991. Line shows abundance in the water column (integrated sample from 0 to 8 m). Positive bars show recruitment rate from the sediment surface and negative bars the sinking rate. White bars show recruitment and sinking at the shallow site (2 m), grey bars show recruitment and sinking at the intermediate site (7 m), and black bars show recruitment and sinking at the deep site (23 m). Note that the sinking rate on 10 July was extreme (-178×10^6 cells·m^{-2}·d^{-1}). Asterisks indicate missing values due to lost traps.

was generally low during January–March. In the beginning of April, the number of rotifers showed a peak (Fig. 3), followed by peaks in small zooplankton in mid-April and in large zooplankton in the beginning of May. The rotifer maximum declined within a month whereas the abundances of *Daphnia* and copepods slowly declined and reached minima in mid-July and September, respectively.

The abundance of *Aphanizomenon* showed one minor peak in abundance in May with about 180×10^3 cells·L^{-1} and a major bloom during June and July with abundances 10 times higher than in May (Fig. 4). In December, a slight increase in abundance occurred. These three humps in the abundance curve corresponded with the recorded maxima in recruitment (Fig. 4). Although the number of cells recruited differed among the stations at 2, 7, and 23 m, maxima and minima generally occurred simultaneously among stations. Sedimentation rate of *Aphanizomenon* filaments was low relative to the recruitment rate during the May and October–November recruitment maxima whereas sedimentation balanced recruitment during the June–July maximum, except for 10 July when the sedimentation rate was more than 30 times the recruitment rate (Fig. 4).

Cryptomonas erosa had its maximum abundance in the water column from early February to late April (Fig. 5). From May to mid-July, *C. erosa* was almost absent from the water column of Lake Mendota. From mid-July to mid-November the abundance was relatively stable at around 10×10^3 cells·L^{-1} (Fig. 5). Of the four selected species, only *C. erosa* showed any recruitment before the end of April (Fig. 5). Recruitment maxima generally corresponded

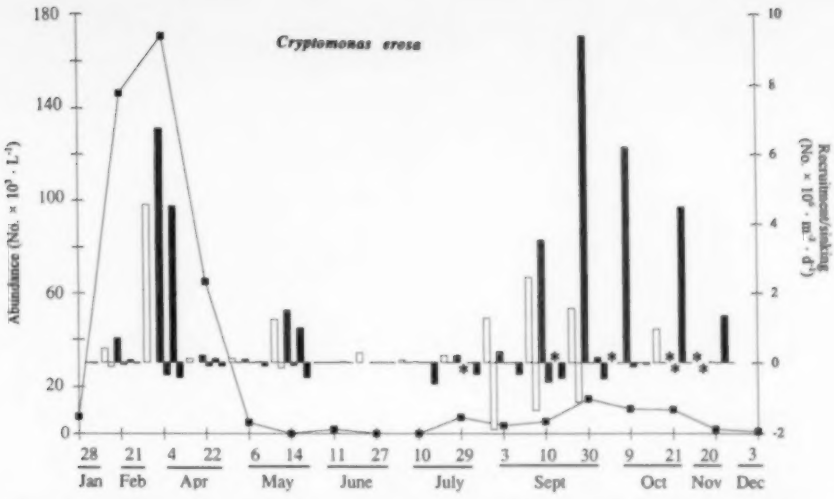


FIG. 5. Population dynamics of *C. erosa* in Lake Mendota during 1991. Line shows abundance in the water column (integrated sample from 0 to 8 m). Positive bars show recruitment rate from the sediment surface and negative bars the sinking rate. White bars show recruitment and sinking at the shallow site (2 m), grey bars show recruitment and sinking at the intermediate site (7 m), and black bars show recruitment and sinking at the deep site (23 m). Asterisks indicate missing values due to lost traps.

to maxima in abundance in the water. During summer and autumn, recruitment maxima did not occur simultaneously at the three stations. Between 3 September and 21 October (maximum 10 September; Fig. 5), *Cryptomonas* was mainly recruited from shallow areas, between 10 September and 7 October from intermediate depths (7 m), and from late October the importance of recruitment from the deep sediments increased (Fig. 5). This dephasing of recruitment patterns did not occur during spring, when patterns were similar and simultaneous among stations (Fig. 5). Sedimentation of *Cryptomonas* was usually moderate compared with recruitment, except at the shallow site during August and September (Fig. 5).

No *Microcystis* were recorded in the water before 27 June when a sudden outbreak occurred with 7×10^6 cells·L^{-1}, followed by a crash 10 d later (Fig. 6). A minor recovery was recorded in late July, whereafter the abundance of *Microcystis* oscillated between 0 and 0.2×10^6 cells·L^{-1} (Fig. 6). Recruitment began in the beginning of June, about 2 wk before the maximum abundance in the water. The major part of the recruitment occurred at the shallow station whereas only small amounts of *Microcystis* were recruited from the intermediate and deep stations (Fig. 6). Except for 27 June, the sinking rate was equal to or higher than the recruitment rate. The maxima in sinking rate in mid-July and end of August corresponded well to the major crashes of the pelagic *Microcystis* population (Fig. 6).

Ceratium hirundinella was either absent or occurred in very low numbers before July and showed maximum abundance in the water column in late August (Fig. 7). By mid-September, the abundance was down at normal and low values (less than 2000 cells·L^{-1}), and after late October, no *Ceratium* were recorded in the lake. Recruitment from the sediment was first recorded on 27 June, 2 wk before the species was recorded in the water column (Fig. 7). Similar to *Cryptomonas*, the recruitment patterns for the different stations were dephased, with recruitment mainly at the shallow station from 27 June to 21 September, followed by the intermediate station from 21 September to 7 October. Finally, one short maximum in recruitment was recorded at the deep station in late October. Maximum sinking rate was recorded during the decline of *Ceratium* in the water during September (Fig. 7).

There was no correlation at the 5% level between wind speed and recruitment if all sampling dates were included ($r < 0.39$; $p > 0.27$). This was also the case when excluding sampling occasions when no cells of the investigated species were present in the water column from the analysis, except for *Microcystis* at the intermediate site ($r = 0.70$; $t = 2.57$; $p < 0.04$).

The recruitment of the four selected species was quantified for the shallow (0–4.5 m), intermediate (4.5–16 m), and deep (16–23 m) intervals, constituting 6, 23, and 71% of the total lake volume and 29, 26, and 45% of the lake area, respectively. On a whole-lake basis, recruitment rarely added more than 1% to the standing stock per day, but in the shallow interval (high area to volume ratio), recruitment occasionally accounted for 6% of the standing stock per day (Table 1).

Discussion

The increase in light extinction coefficient (higher light attenuation) in Lake Mendota during March and April 1991 corresponded to high abundances in *Cryptomonas* and diatoms whereas the high extinction coefficients during June and July corresponded to population maxima in *Microcystis* and *Aphanizomenon*.

The extremely high sedimentation rate of *Aphanizomenon* at the shallow site around 10 July corresponded with the crash of the population between 10 and 29 July. The reason for this rapid late summer decline is unknown, but constitutes

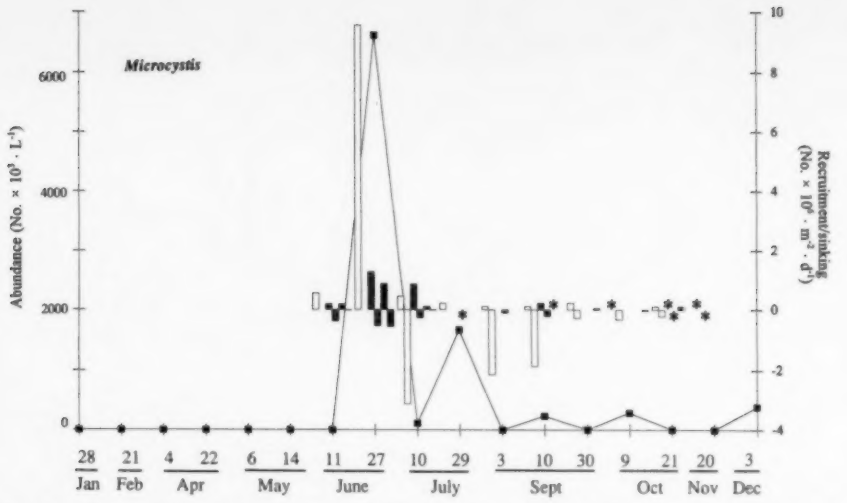


FIG. 6. Population dynamics of *M. aeruginosa* in Lake Mendota during 1991. Line shows abundance in the water column (integrated sample from 0 to 8 m). Positive bars show recruitment rate from the sediment surface and negative bars the sinking rate. White bars show recruitment and sinking at the shallow site (2 m), grey bars show recruitment and sinking at the intermediate site (7 m), and black bars show recruitment and sinking at the deep site (23 m). Asterisks indicate missing values due to lost traps.

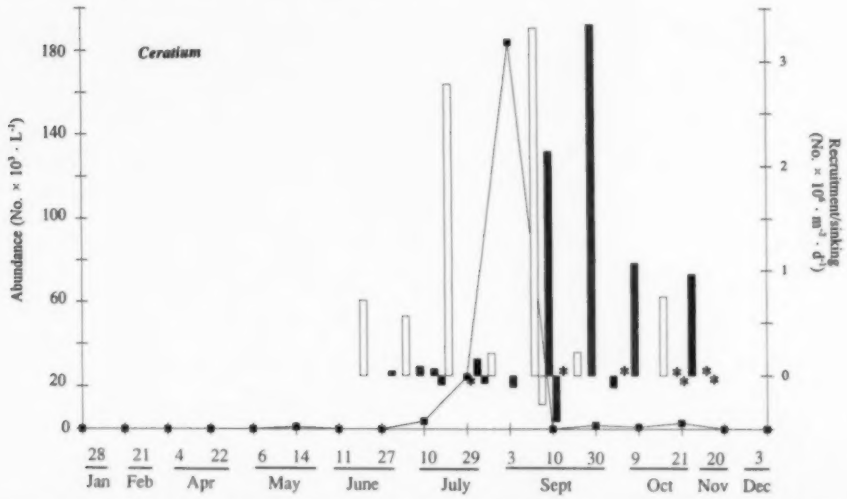


FIG. 7. Population dynamics of *C. hirundinella* in Lake Mendota during 1991. Line shows abundance in the water column (integrated sample from 0 to 8 m). Positive bars show recruitment rate from the sediment surface and negative bars the sinking rate. White bars show recruitment and sinking at the shallow site (2 m), grey bars show recruitment and sinking at the intermediate site (7 m), and black bars show recruitment and sinking at the deep site (23 m). Asterisks indicate missing values due to lost traps.

a regular phenomenon in Lake Mendota (Fallon and Brock 1980). Sinking rate was low during the first recruitment maximum of *Aphanizomenon* in May, but equal to the recruitment rate at the intermediate and deep sites during recruitment maxima in June and July (Fig. 4). One explanation is that this later recruitment was successful and that the high sinking rate was caused by a pelagic population that was beginning to decline. Another possibility is that the recruitment in June–July was unsuccessful (recruitment balanced sinking, i.e., no net recruitment; Fig. 4) because stratification (that was completely established 31 May) physically or chemically affected the migration to the euphotic zone. If so, recruitment to the euphotic zone may have been successful only during May, and the population maximum in the water during June and July originated mainly from the May recruitment period.

TABLE 1. Number of cells/colonies recruited (R) per day from the sediment surface of Lake Mendota during selected days with high recruitment rates of *A. flos-aquae*, *C. erosa*, *M. aeruginosa*, and *C. hirundinella*. Recruitment was recorded at 2, 7, and 23 m water depth, representing the depth intervals 0–4.5 m (29% of the total area), 4.5–16 m (26%), and 16–23 m (45%). Whole-lake recruitment constitutes the sum of the recruitment in each interval. Total number of cells/colonies in the water on the selected sampling days is also given for each interval, assuming that an integrated sample from 0 to 8 m water depth is an estimate of the cell number throughout the water column. Recruitment is also calculated as the portion (%·24 h^{-1}) of the total cell number in the water. Due to a lost trap the recruitment rate of *Ceratium*, 30 July is estimated as the mean of the recruitment rates at the shallow and deep sites.

		Interval (m):	0–4.5	4.5–16	16–23	0–23
		Area ($\times 10^6$ m^2):	11.2	10.5	17.5	39.1
		Volume ($\times 10^6$ m^3):	27	110	349	486
	Day		Shallow	Intermediate	Deep	Whole lake
Aphanizomenon	6 May	R($\times 10^{14}$·d^{-1})	1.2	2.5	1.2	4.8
		No. ($\times 10^{14}$)	35	143	454	632
		%	3.3	1.7	0.3	0.8
	12 July	R($\times 10^{14}$·d^{-1})	0.6	1.4	1.1	3.1
		No. ($\times 10^{14}$)	5	20	63	88
		%	0.1	<0.1	<0.1	<0.1
Cryptomonas	6 April	R($\times 10^{14}$·d^{-1})	0.5	0.6	0.8	2.0
		No. ($\times 10^{14}$)	45	187	593	826
		%	1.2	0.4	0.1	0.2
	27 Sept.	R($\times 10^{14}$·d^{-1})	0.2	1.0	0.03	1.2
		No. ($\times 10^{14}$)	3.9	16	52	68
		%	4.6	6.0	<0.1	1.8
Microcystis	27 June	R($\times 10^{14}$·d^{-1})	1.1	0.1	0.2	1.4
		No. ($\times 10^{14}$)	1780	7260	23030	32070
		%	<0.1	<0.1	<0.1	<0.1
	12 July	R($\times 10^{14}$·d^{-1})	0.05	0.09	0.02	0.16
		No. ($\times 10^{14}$)	30	121	384	535
		%	0.2	0.1	<0.1	<0.1
Ceratium	12 July	R($\times 10^{14}$·d^{-1})	0.06	0.01	0.01	0.08
		No. ($\times 10^{14}$)	1	4	13	18
		%	6.1	0.2	<0.1	0.4
	30 July	R($\times 10^{14}$·d^{-1})	0.3	0.2	0.03	0.50
		No. ($\times 10^{14}$)	7	27	85	119
		%	4.9	0.6	<0.1	0.4

Interpolation of the recruitment data from the three depths may give a rough estimate of the importance of algal recruitment for the pelagic populations of the investigated algae. Despite high recruitment rates in June and July, less than 0.1% of the standing stock was added through recruitment during this period (Table 1), further indicating that recruitment in May constituted the inoculum for the bloom in June and July (Fig. 4). A parallel case is the slight increase in *Aphanizomenon* filaments in the water column following a few weeks after the modest recruitment period in October and November when the lake was completely mixed, again suggesting that recruitment of *Aphanizomenon* in Lake Mendota operates mainly as inoculum for future growth.

The use of any trapping device for quantifying biomass or transport of organisms usually introduces artefacts. The major concern with respect to the funnel traps used in the present study is the possibility that algae caught in the traps are not recruits from the sediment, but simply planktonic cells passively transported by currents. There are, however, several observations suggesting that this is unlikely. (1) Water currents are higher at high wind speed, suggesting that recruitment generally should be higher at high wind speed. With one exception (*Microcystis* at the intermediate site, $r = 0.70$; $p < 0.04$; $n = 9$), there was never any relationship between wind speed and recruitment for any of the investigated species. (2) Funnel traps set inside plastic enclosures (i.e., no influence of currents) gave recruitment and sinking rates in the same order of magnitude as in the present study (see Hansson 1993). (3) Some algal groups, e.g., diatoms, were often common in the water column, but rarely found in the recruitment traps (although present in sinking traps during population crashes). These observations do not show that currents or resuspension are unimportant vectors for the vertical transport of algae, but indicate that they may not have been major artefacts in the quantification of algal recruitment in Lake Mendota. Instead, the temporal and spatial differences in recruitment among species, in combination with the fact that only some of the species present in the lake were found in the traps, suggest that recruitment is mainly an active process.

Ceratium hirundinella is able to form resting cysts on the sediment surface (Heaney et al. 1983). In a eutrophic pond, Heaney et al. (1983) recorded an 18-fold increase in vegetative *Ceratium* within a week simultaneously with the presence of empty cysts on the sediment surface, indicating that encystment directly affected cell numbers in the water. In their study pond, encystment, and the following increase in cell number, occurred when the temperature at 1 m depth increased from 3 to 5°C. In Lake Mendota, neither recruitment nor an increase in cell number in the water occurred before the surface water temperature had reached 24°C, suggesting that temperature is not the general triggering factor for the recruitment of *Ceratium*.

Microcystis is known to form dense overwintering mats on the sediment surface during fall and winter, which constitute the inoculum for the coming year's pelagic population in many lakes (Sirenko 1987), including Lake Mendota (Fallon and Brock 1981). The *Microcystis* colonies caught in our funnel traps likely originated from such vegetative mats. In late June, *Microcystis* showed the only recruitment period of significance during 1991 (Fig. 6). The sudden crash of the pelagic *Microcystis* population between 27 June and 10 July occurred simultaneously with an increase in the abundance of *Aphanizomenon*. In a Swedish eutrophic lake, recruitment of *Aphanizomenon* occurred before and after, but not during, the recruitment maximum of *Microcystis* (personal observations). Such temporal adjustments in abundance and recruitment patterns may be an indication of competitive interactions between different cyanophytes.

The increase of the anoxic zone during stratification has been suggested to initialize the recruitment of cyanophytes (Trimbee and Prepas 1988). In Lake Mendota, no recruitment of *Microcystis* occurred before the onset of stratification (Fig. 2 and 6), which supports this hypothesis. However, the main recruitment occurred at the shallow site, far from anoxic water. The recruitment of *Aphanizomenon* had already begun at the beginning of May, when the concentration of dissolved oxygen at the sediment surface (23 m) was above 10 $mg \cdot L^{-1}$. Furthermore, in March the oxygen concentration was close to zero (0.4 $mg \cdot L^{-1}$), but no recruitment of either *Aphanizomenon* or *Microcystis* occurred. Hence, the suggestion that anoxic conditions per se are the initializing factor for cyanophyte recruitment from sediment to water is not corroborated by our results.

The lake stratified between 7 and 20 May and was completely mixed again by 7 October. The thermocline fluctuated between 6 and 12 m water depth, indicating that our intermediate station at 7 m depth sometimes was above and sometimes below the thermocline. Only *Aphanizomenon* showed any significant recruitment at the deep or intermediate sites during stratification, which may have been an unsuccessful colonization because the sinking rates were as high as recruitment rates. *Ceratium* and *Microcystis* showed high recruitment rates at the shallow site (above the thermocline), but low rates at the intermediate and deep sites during stratification. After about 6 September, when the thermocline was below 10 m, the recruitment of *Ceratium* and *Cryptomonas* from the intermediate site increased. When the lake was again mixed after 7 October, recruitment of *Aphanizomenon*, *Cryptomonas*, as well as *Ceratium* was initiated at the deep site (Fig. 4, 5, and 7). Hence, it may be suggested that a variable associated with stratified conditions reduced the upward migration. This factor may either be a chemical substance associated with stratified conditions or the thermocline itself may function as a physical "lid" for recruitment to the euphotic zone. The latter notion is in contrast with the observed diurnal migrations of *Cryptomonas marssonii* through temperature gradients of 10°C in a small Finnish lake (Salonen et al. 1984), as well as with studies on *Oscillatoria* (Klemer 1976; Konopka et al. 1993). However, with the exception of *Aphanizomenon*, none of the species investigated in Lake Mendota even attempted to colonize the water column from below the thermocline during stratification, but instead seemed to stay on the sediment surface until stratification was broken. A possibility is that algae have receptors detecting, for example, oxygen concentrations, indicating a thermocline impossible to penetrate. The existence of such receptors may explain why most algae avoided migration to the planktonic habitat during stratification. The onset of recruitment when stratification was broken may be a passive phenomenon induced by mixing currents. However, maximum recruitment at the intermediate and deep sites should then occur as a short pulse during the breakup of stratification, which was not the case. Another possibility is that habitat shift from sediment to water is actively regulated by the algae, e.g., by means of chemoreceptors monitoring environmental variables. As stratified conditions seem to be associated with low rates of vertical migration, possible variables may be low oxygen and high phosphate concentrations. In line with this notion, the recruitment rate of *C. erosa* was positively correlated with the oxygen concentration at the sediment surface at the deep site ($r = 0.57$; $t = 2.302$; $p < 0.042$). Moreover, experimental field studies have shown that phosphorus additions reduce the buoyancy of *Oscillatoria* filaments (Konopka et al. 1978).

Although the thermocline may affect migration from hypolimnetic sediments, algae recruited from epilimnetic sediments are able to colonize the whole water column via horizontal currents. This is particularly illustrated by *Ceratium* that showed recruitment almost exclusively from shallow areas during summer followed by a peak in abundance during late July and early August.

The recorded sedimentation of *Cryptomonas* was usually low, indicating that other factors were important for the decline in cell numbers, such as grazing or decomposition before reaching the sediment surface. The increase in grazer abundance during April (Fig. 3) coincided with the rapid decline in *Cryptomonas* abundance, suggesting that grazing may have caused the decrease in cell numbers of *Cryptomonas* during this period. Including *Daphnia* abundance and the concentration of oxygen as independent variables in a multiple regression explained 48% of the variation in recruitment of *Cryptomonas* ($F = 4.56$; $p < 0.039$). An even higher explanatory value ($r^2 = 0.54$; $F = 5.95$; $p < 0.020$) is revealed if *Daphnia* is substituted with the abundance of small zooplankters (copepods). This negative relationship between grazer abundance and recruitment indicates that *Cryptomonas* avoided shifting habitat from sediment to water during high grazer abundances (Hansson 1993). However, we cannot rule out the alternative explanation that grazing between the sediment surface and the trap (a distance of 0.75 m) caused a reduction in the observed recruitment of *Cryptomonas*. There was a positive correlation between grazer (*Daphnia*) abundance and recruitment of *Aphanizomenon* ($r = 0.57$; $t = 2.470$; $p < 0.028$), an observation in line with

the suggestion that *Daphnia* may positively affect bloom formation of *Aphanizomenon* (Shapiro 1980). There was no relationship between grazer abundance or oxygen concentration and recruitment rates of *Microcystis* or *Ceratium*.

The major part of the recruitment periods of the four investigated species was successful (i.e., mirrored in population increases), suggesting that algae are able to temporally adjust their recruitment toward favourable periods. The relationships between recruitment rates and such diverse factors as oxygen concentration, stratification, and grazer abundance indicate that habitat shift from sediment to water is not regulated by a single factor. It is also obvious that recruitment of different species is governed by different factors. The understanding of these processes is an important tool in predicting and managing algal blooms.

Acknowledgments

This study was funded in part by the Federal Aid in Sport Fish Restoration Act under Project F-95-P, the Wisconsin Department of Natural Resources, and the Swedish Natural Science Research Council (NFR; to L.-A.H.). Water column data collection was done in cooperation with R. Lathrop, Wisconsin Department of Natural Resources. We thank S.R. Carpenter and J.F. Kitchell for support and encouragement during the study and S.R. Carpenter for valuable comments on the manuscript.

References

Barbiero, R. 1993. A contribution to the life history of the planktonic cyanophyte, *Gloeotrichia echinulata*. Arch. Hydrobiol. 127: 87–100.

Barbiero, R., and E. Welch. 1992. Contribution of benthic blue-green algal recruitment to lake populations and phosphorus translocation. Freshwater Biol. 27: 249–260.

Birge, E., and C. Juday. 1922. The inland lakes of Wisconsin. The plankton. I. Its quantity and chemical composition. Wis. Geol. Nat. Hist. Surv. Bull. Sci. Ser. 13. 64: 1–22.

Brock, T. 1985. A eutrophic lake — Lake Mendota, Wisconsin. Ecological Studies. Springer-Verlag. New York, N.Y.

Crumpton, W. 1987. A simple and reliable method for making permanent mounts of phytoplankton for light and fluorescence microscopy. Limnol. Oceanogr. 32: 1154–1159.

Cullen, J., and S. Horrigan. 1981. Effects of nitrate on the vertical migration, carbon to nitrogen ratio, and the photosynthetic capacity of the dinoflagellate *Gymnodinium splendens*. Mar. Biol. 62: 81–89.

Fallon, R., and T. Brock. 1980. Planktonic blue-green algae: production, sedimentation, and decomposition in Lake Mendota, Wisconsin. Limnol. Oceanogr. 25: 72–88.

Fallon, R., and T. Brock. 1981. Overwintering of *Microcystis* in Lake Mendota. Freshwater Biol. 11: 217–226.

Hansson, L-A. 1993. Factors initiating algal life-form shift from sediment to water. Oecologia 94: 286–294.

Heaney, S, D. Chapman, and H. Morison. 1983. The role of the cyst stage in the seasonal growth of the dinoflagellate *Ceratium hirundinella* within a small productive lake. Br. Phycol. J. 18: 47–59.

Kitchell, J. [ed.] 1992. Food web management — A case study of Lake Mendota. Springer-Verlag. New York, N.Y.

Klemer, A. 1976. The vertical distribution of *Oscillatoria agardhii* var. *isotrix*. Arch. Hydrobiol. 78: 343–362.

Klemer, A., and A. Konopka. 1989. Causes and consequences of blue-green algal (cyanobacterial) blooms. Lake Reservoir Manage. 5: 9–19.

Konopka, A., T. Brock, and A. Walsby. 1978. Buoyancy regulation by planktonic blue-green algae in Lake Mendota, Wisconsin. Arch. Hydrobiol. 83: 524–537.

Konopka, A., A. Klemer, A. Walsby, and B. Ibelings. 1993. Effects of macronutrients upon buoyancy regulation by metalimnetic *Oscillatoria agardhii* in Deming Lake, Minnesota. J. Plankton Res. 16: 1019–1034.

Kromkamp, J., A. Konopka, and R. Mur. 1988. Buoyancy regulation in light limited continuous cultures of *Microcystis aeruginosa*. J. Plankton Res. 10: 171–183.

Lund, J.W.G. 1954. The seasonal cycle of the plankton diatom *Melosira italica* (EHR) Kütz, subspesies *subarctica* o. Müll. J. Ecol. 42: 151–179.

Osgood, R. 1988. A hypothesis on the role of *Aphanizomenon* in translocating phosphorus. Hydrobiologia 169: 69–76.

Pettersson, K., E. Herlitz, and V. Istvánovics. 1993. The role of *Gloeotrichia echinulata* in the transfer of phosphorus from sediment to water in Lake Erken. Hydrobiologia 253: 123–129.

Reynolds, C. 1972. Growth, gas vacuolation and buoyancy in a natural population of a planktonic blue-green alga. Freshwater Biol. 2: 87–106.

Reynolds C., and A. Walsby. 1975. Water blooms. Biol. Rev. 50: 437–481.

Salonen, K., R. Jones, and L. Arvola. 1984. Hypolimnetic phosphorus retrieval by diel vertical migration of lake phytoplankton. Freshwater Biol. 14: 431–438.

Schmidt, W. 1928. Über Temperatur und Stabilitätsverhältnisse von Seen. Geog. Ann. 10: 145–177.

Shapiro, J. 1980. The importance of trophic-level interactions to the abundance and species composition of algae in lakes. *In* J. Barica and L. Mur [ed.] Hypertrophic ecosystems. Developments in hydrobiology 2. Dr. W. Junk, The Hague, The Netherlands.

Sirenko, L. 1987. The effect of blue-green algae on formation of algal communities and on water cuality in the Dnieper reservoirs. Arch. Hydrobiol. Beih. Ergebn. Limnol. 25: 39–49.

Trimbee, A., and E. Prepas. 1988. The effect of oxygen depletion on the timing and magnitude of blue-green algal blooms. Verh. Int. Ver. Limnol. 23: 220–226.

Walsby, A., and A. Klemer. 1974. The role of gas vacuols in the microstratification of a population of *Oscillatoria agardhii* var. *isotrix* in Derming Lake, Minnesota. Arch. Hydrobiol. 74: 375–392.

Overwintering of Adult Northern Atlantic Cod (*Gadus morhua*) in Cold Inshore Waters as Evidenced by Plasma Antifreeze Glycoprotein Levels

Sally V. Goddard

Marine Sciences Research Laboratory, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada

J.S. Wroblewski

Fisheries Oceanography Group, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada

C.T. Taggart

Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, NF A1C 5X1, Canada

K.A. Howse and W.L. Bailey

Fisheries Oceanography Group, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada

and M.H. Kao and G.L. Fletcher

Ocean Sciences Centre and Department of Biology, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada

Goddard, S.V., J.S. Wroblewski, C.T. Taggart, K.A. Howse, W.L. Bailey, M.H. Kao, and G.L. Fletcher. 1994. Overwintering of adult Northern Atlantic cod (*Gadus morhua*) in cold inshore waters as evidenced by plasma antifreeze glycoprotein levels. Can. J. Fish. Aquat. Sci. 51: 2834–2842.

Adult Atlantic cod (*Gadus morhua*) are known to produce antifreeze glycoproteins in response to cold temperatures. Our laboratory studies demonstrated that blood plasma levels in adult cod were positively correlated with the number of days they spent in subzero water. Between April 1991 and June 1993, we monitored concentrations of antifreeze glycoproteins in the plasma of late juvenile and adult cod in Trinity Bay, Newfoundland, and used the results to estimate how long cod had been exposed to low water temperatures. A consideration of these data in conjunction with detailed temperature profiles of the area taken over the course of the study allowed us to deduce the distribution of cod in relation to the temperature field. This study provides evidence that (1) blood antifreeze glycoprotein levels can be used to deduce the recent thermal history of cod in the wild and (2) after their inshore summer feeding period, considerable numbers of adult cod overwintered inshore in Trinity Bay in subzero water, producing antifreeze glycoproteins as temperatures fell below 0°C. From May onwards, "cold-adapted" cod moved into warming surface waters, where they became available to an early inshore trap fishery.

Il a été établi que les morues franches (*Gadus morhua*) adultes produisent des glycoprotéines antigels quand elles sont exposées au froid. Nous avons démontré en laboratoire l'existence d'une corrélation positive entre les taux de ces protéines dans le plasma sanguin de morues adultes et le nombre de jours que ces dernières passaient dans de l'eau à une température inférieure à 0°C. D'avril 1991 à juin 1993, nous avons mesuré les concentrations de glycoprotéines antigels dans le plasma de morues pré-adultes et adultes de la baie Trinité, à Terre-Neuve, et estimé à partir des résultats obtenus le temps d'exposition de ces poissons à de basses températures. L'examen des données recueillies et des profils détaillés de température établis dans la région durant la période de l'étude nous a permis de déduire la répartition des morues en rapport avec le champ de température. Les conclusions de l'étude sont les suivantes : 1) les concentrations sanguines de glycoprotéines antigels peuvent être utilisées pour déduire l'exposition thermique récente des morues dans leur milieu naturel et 2) après leur période d'alimentation estivale dans les eaux côtières, un grand nombre de morues adultes avaient hiverné dans les eaux côtières de la baie Trinité, exposées à des températures inférieures à 0°C, ce qui leur faisait produire des glycoprotéines antigels. À partir du mois de mai, les morues « adaptées au froid » ont gagné les eaux de surface, qui commençaient alors à se réchauffer, et pouvaient ainsi faire l'objet d'une pêche côtière printanière à la trappe.

Received August 18, 1993
Accepted May 30, 1994
(J12057)

Reçu le 18 août 1993
Accepté le 30 mai 1994

Atlantic cod (*Gadus morhua*) in the wild generally inhabit waters ranging in temperature from −0.5 to 10°C (Rose and Leggett 1988; Scott and Scott 1988). However, field observations of cod distribution in relation to temperature suggest that their optimal thermal range is between 0 and 5°C (Beverton and Lee 1965; Templeman and May 1965; Lear et al. 1986; Rose and Leggett 1988). Further, Taggart and Frank (1987) gave 2.9°C as the median

temperature for highest cod catches in the Northwest Atlantic and elsewhere.

The adult and juvenile Atlantic cod studied in this work were from the Northern cod stock, defined as those cod populations inhabiting NAFO Divisions 2J, 3K, and 3L off the coast of Newfoundland and Labrador. They will be referred to throughout as Northern cod, or simply cod.

The pattern of migration accepted for the majority of Northern cod allows them to inhabit their optimal thermal range throughout the year (Templeman 1966; Lear and Green 1984; Lear et al. 1986). Adult Northern cod are described leaving inshore summer feeding grounds by late fall – early winter to overwinter offshore in warm (>2°C), deep water below the cold intermediate layer (Petrie et al. 1988). Spawning takes place in spring and is followed by an inshore migration to summer feeding grounds (Templeman 1966). Once inshore, the cod feed primarily on capelin (*Mallotus villosus*), become replenished, and move offshore at the end of the summer to repeat the cycle (Lear and Green 1984; Lear et al. 1986). By overwintering offshore, adult cod avoid exposure to the potentially lethal combination of very low water temperatures (down to −1.8°C) and ice that is a regular winter occurrence in the coastal seas of Newfoundland (Templeman 1966; Symonds 1986; Davies et al. 1988; Petrie et al. 1988; Fissel and Tang 1991).

However, there is evidence to suggest that some adult cod overwinter inshore in Newfoundland bays where water temperatures regularly fall below zero during the winter months (Templeman and Fleming 1965; Wroblewski et al. 1994). Have these fish spent the winter inhabiting cold water, or have they mainly confined themselves to local inshore areas of deep warm water as suggested by Thompson (1943), making only short-duration feeding sorties into the predominantly subzero waters of the bays?

Because continuous monitoring of the overwintering behaviour of significant numbers of free-roaming cod is not practical, the development of alternative methods, such as the use of biochemical or physiological indicators of thermal history, is desirable. We suggest that measuring antifreeze levels in blood plasma is one such appropriate technique.

When exposed to low temperatures, cod produce glycoproteins which are found in the blood and other extracellular fluids. These are termed antifreeze glycoproteins because they increase the freeze resistance of the fish by lowering the plasma freezing point from usual summer values of between −0.6 and −0.8°C (both juveniles and adults) to approximate mean values of −1.5°C in juvenile and −1.2°C in adult cod (Hew et al. 1981; Fletcher et al. 1987; Kao and Fletcher 1988; Goddard et al. 1992). In addition, experiments suggest that antifreeze proteins/glycoproteins protect the integrity of cell membranes at low temperatures (Rubinsky et al. 1990, 1991; Negulescu et al. 1992). This dual function of antifreeze would appear to be of considerable survival value to cod living in very cold, possibly icy waters.

Antifreeze levels in adult cod appear to be regulated entirely by water temperature. When adults are continuously exposed to temperatures of 0°C and below during winter, antifreeze glycoproteins appear in the blood and increase to maximal levels over a period of months, significantly lowering the plasma freezing point. The loss of antifreeze is also temperature dependant. As water temperatures rise above 0°C after the winter, blood antifreeze levels decline until eventually no antifreeze can be detected in the plasma (Fletcher et al. 1987). While antifreeze has, on occasion, been found in the plasma of adult cod acclimated to temperatures between 0 and 2°C, levels have always been low and transitory (Fletcher et al. 1987; S.V. Goddard and G.L. Fletcher, unpublished data). With certain provisos (see Discussion) the relationships between water temperature and the level of plasma antifreeze can be used in the following way to deduce the thermal history of adult cod in the field. First, the presence of significant levels of antifreeze in the blood (sufficient to produce a >0.1°C difference between the freezing and melting point of the plasma) indicates acclimation to 0°C or below. Second, the antifreeze concentration gives an indication of how long the cod have been exposed to cold water. Third, as warm (>0°C) water becomes available to cold-adapted fish (either by migration to other areas or by solar warming in the area occupied), we can estimate the length of time fully cold-adapted cod have been exposed to temperatures above 0°C by the rate of loss of antifreeze from the plasma.

In this study, we have (1) developed a plasma antifreeze/water temperature calibration to estimate the length of time cod have been exposed to low water temperatures, (2) measured the plasma antifreeze levels in cod caught at different times of the year in Trinity Bay, Newfoundland, and the temperature of the water from which they were collected, and (3) used these data, coupled with temperature data obtained from a long-term oceanographic monitoring program in the area, to deduce the thermal history (weeks–months) and distribution, with respect to temperature, of cod in Trinity Bay.

Materials and Methods

General Collection and Analysis of Blood Samples

All blood samples (1–2 mL) were taken from a caudal blood vessel using 3-cc syringes fitted with 21- or 23-gauge needles. Sampling usually took less than 1 min and no anaesthetic was used. Blood samples were placed in Vacutainers containing sodium heparin (Becton Dickinson) and centrifuged for 10 min at 4000*g* to separate cells from plasma. Plasma samples were then stored at −20°C until analysed.

Antifreeze activity was assessed using a nanolitre osmometer (Clifton Technical Physics, Hartford, N.Y.). With this technique, a single ice crystal within the plasma sample is observed under a microscope, and by fine temperature adjustments within the stage holding the sample, the plasma freezing and melting points can be obtained. The difference between the freezing and melting temperature is termed thermal hysteresis and is a direct measure of antifreeze activity (Kao et al. 1986).

Collection of Blood Samples from Cod Held in Laboratory Raceways

From 1984 to 1991, adult cod were collected during the summer (July and August) cod trap fishery in Conception Bay, Newfoundland. From summer until June the following year, these fish were held under ambient light and temperature conditions in a 40 000-L raceway supplied with running seawater pumped directly from a depth of 5–10 m in Logy Bay at the laboratory location (Fletcher et al. 1987). These raceway-held cod were exposed to subzero temperatures from January to April, with plasma antifreeze levels typically

TABLE 1. Sampling dates and days of exposure to subzero temperatures for cod held in the laboratory raceway. Length of exposure to subzero temperatures was obtained by subtracting the Julian day on which the water temperature in the raceway fell below 0°C from the sampling date (Julian days). n = number of fish sampled.

Sampling date	Subzero exposure (d)	n
Jan. 9, 1991	2	10
Jan. 13, 1988	6	11
Jan. 18, 1991	11	9
Jan. 17, 1985	15	8
Jan. 25, 1991	18	9
Jan. 27, 1986	25	6
Jan. 30, 1984	28	5
Feb. 5, 1991	29	10
Jan. 31, 1989	32	7
Feb. 24, 1988	48	18
Feb. 27, 1985	56	10
Feb. 29, 1984	58	5
Mar. 13, 1985	70	5
Mar. 18, 1991	70	10
Mar. 15, 1989	75	10

reaching peak values by mid-March and declining between April and June as water temperatures increased (Fletcher et al. 1987; Goddard et al. 1992). The date on which the water temperature in the raceway first fell below 0°C each winter was recorded (between December 28 and January 7 in all years considered).

During the rising phase of antifreeze production (January–mid-March), blood samples were collected from raceway-held cod. The sampling dates were converted into length of exposure of the animals to subzero temperature. The sampling schedule is presented in Table 1.

Collection of Blood Samples from Cod in the Field

Cod sampled in the field were separated into juvenile (<40 cm) and late juvenile/adult (40+ cm) length categories. The physiology of antifreeze production appears to differ in juvenile and adult cod (Kao and Fletcher 1988; Goddard et al. 1992). Therefore, only data from the latter group were compared with data derived from adult cod held in the laboratory raceway.

Blood samples were collected from cod at a variety of sites (see Fig. 1) in the Random Island area of Trinity Bay on the following dates.

April 8, 1991

Forty seven cod (length 37.5–88.9 cm, 45 fish 40+ cm) were caught in Hatchet Cove, Southwest Arm, with baited longlines (six fish) and gill nets (41 fish). Fish were caught at depths greater than 150 m at water temperatures of −0.6 to −0.7°C.

May 1, 1992

Twenty cod (length 38.7–53.3 cm, 18 fish 40+ cm) were caught in a cod trap in Resolution Cove, Smith Sound. The fish were in the top 20 m of the water at temperatures between 0 and 1°C.

May 28, 1992

Twenty-six cod (length 39.8–49.3 cm, 25 fish 40+ cm) were caught in a cod trap in Nut Cove, Smith Sound. Fish were in the top 40 of the water at temperatures between 1.8 and 3.7°C. Subsequent to blood sampling, these fish were transported to the laboratory, tagged, and held in the raceway under seasonally ambient conditions of temperature and photoperiod until July 29, 1992, when blood samples were again taken from the remaining 17 live fish. During this period, raceway temperatures were taken several times a week.

June 18–20, 1992

Thirty-nine cod (length 29.0–67.0 cm, 26 fish 40+ cm) were caught by otter trawling along the bottom of Southwest Arm at depths of 150–180 m and water temperatures between −0.9 and −1.3°C.

June 29–30, 1992

Twenty-six cod (length 26.0–83.0 cm, 12 fish 40+ cm) were caught by jigging in approximately 40 m of water in Newman Sound, Bonavista Bay (see Fig. 1, inset).

September 30 – October 1, 1992

Forty-four cod (length 26.0–49.0 cm, 10 fish 40+ cm) were caught at St. Jones Within, Southwest Arm, either by jigging in 40 m of water (12 fish) or in a capelin trap set in 20 m of water (32 fish). Surface temperatures were approximately 12°C, while temperatures at 40 and 20 m were 2.3 and 8.0°C, respectively. At this time, no cod were caught by otter trawling along the entire length of Southwest Arm. Bottom temperatures along the trawl path ranged from −1.3 to 0°C.

June 2–5, 1993

Sixty-one cod (length 27.0–51.0 cm, 26 fish 40+ cm) were caught by otter trawling in Southwest Arm at depths from 139 to 174 m and temperatures from −0.9 to −1.2°C. This was essentially a repeat of our June 1992 sample.

Temperature Measurements in the Field

Temperature sections were taken in Southwest Arm on January 24, 1991, and out into the deep water of Trinity Bay on January 27–28, 1991. On March 13, 1991, in the Hatchet Cove area of Southwest Arm, temperature/depth profiles were taken both at the edge (to 40 m approximate depth) and half way across (to 160 m approximate depth) the Arm. In all cases, temperatures were recorded with a VEMCO Ltd. Sealog-TD temperature/depth recorder (accuracy = ±0.1°C/±5 m). In addition, between March 1991 and August 1992, water temperatures in the Random Island area of Trinity Bay were monitored in sufficient detail to allow production of monthly temperature sections for Southwest and Northwest Arm (Wroblewski et al. 1993).

Temperatures and depths of capture were recorded on each occasion that cod were collected for blood sampling. Vertical temperature profiles were taken when gill nets, longlines, jiggers, or traps were used. When using the otter trawl, temperature/depth profiles were taken on completion of the tows at either end of the tow path using a wire-mounted Sea-Bird Electronics Inc. Seacat SBE 19-03. The Sea-Bird Seacat equipment was used to take temperature/depth profiles on June 18–20, 1992, June 29–30, 1992, September 30 – October 1, 1992, and June 2–5, 1993, while the VEMCO Sealog equipment was used on April 8, 1991, May 1, 1992, and May 28, 1992.

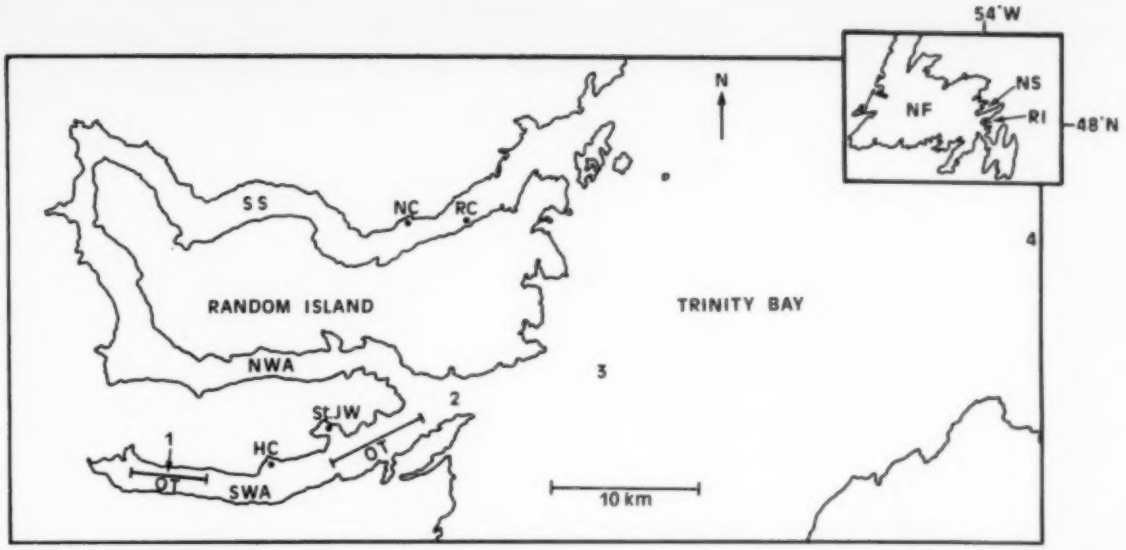


FIG. 1. Chart of the Random Island area of Trinity Bay, Newfoundland, showing transect line (1,2,3,4) along which temperature stations were located. SWA, Southwest Arm; NWA, Northwest Arm; SS, Smith Sound; five fish capture sites, namely HC (Hatchet Cove, April 8, 1991), RC (Resolution Cove, May 1, 1992), NC (Nut Cove, May 28, 1992), OT (Southwest Arm, otter trawl path, June 18–20, 1992, and June 2–5, 1993). St.JW (St. Jones Within, September 30 – October 1, 1992). Inset chart shows location of Random Island (RI) in Trinity Bay, relative to Newman Sound (NS) in Bonavista Bay, where cod were sampled on June 29–30, 1992.

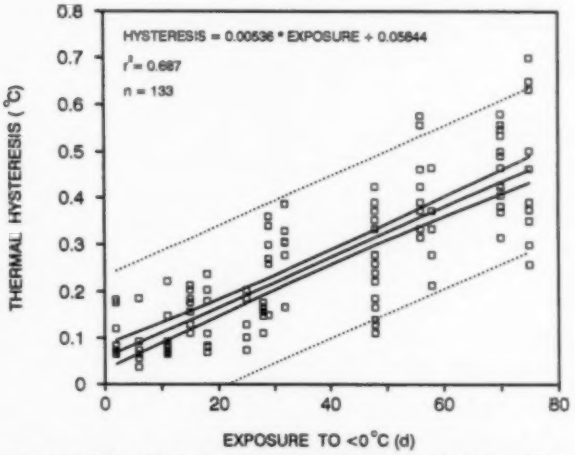


FIG. 2. Relationship between plasma antifreeze levels (thermal hysteresis) and the length of time that adult cod had been living at subzero temperatures. Solid lines are the 95% confidence limits around the regression; dotted lines are the 95% prediction limits for thermal hysteresis in individuals from a sample population of known subzero exposure time.

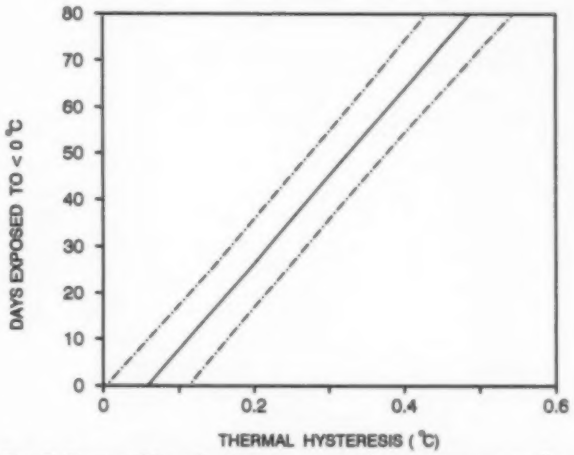


FIG. 3. Expected length of exposure to subzero temperatures for a measured mean value of thermal hysteresis (graph derived from the relationship given in Fig. 2 using inverse prediction statistics). Broken lines are the 95% confidence limits for the expected values for length of exposure of a sample population.

Results

Laboratory Observations

In adult cod held under ambient temperature and light conditions, blood plasma thermal hysteresis (antifreeze) levels were significantly correlated with the duration of exposure to subzero temperature during the rising phase of antifreeze production (Fig. 2). Mean maximal levels of thermal hysteresis (0.46°C) were reached by mid-March, approximately 75 d after first exposure to subzero temperatures. Using the inverse prediction statistics (estimation of X from Y) outlined by Sokal and Rohlf (1981), this relationship can be used as a first approximation in deducing the thermal history of cod in the wild (Fig. 3).

Field Observations

Temperature sections taken at the end of January 1991 showed that while much of the surface water and some of the bottom water in Trinity Bay was below 0°C, a large lens

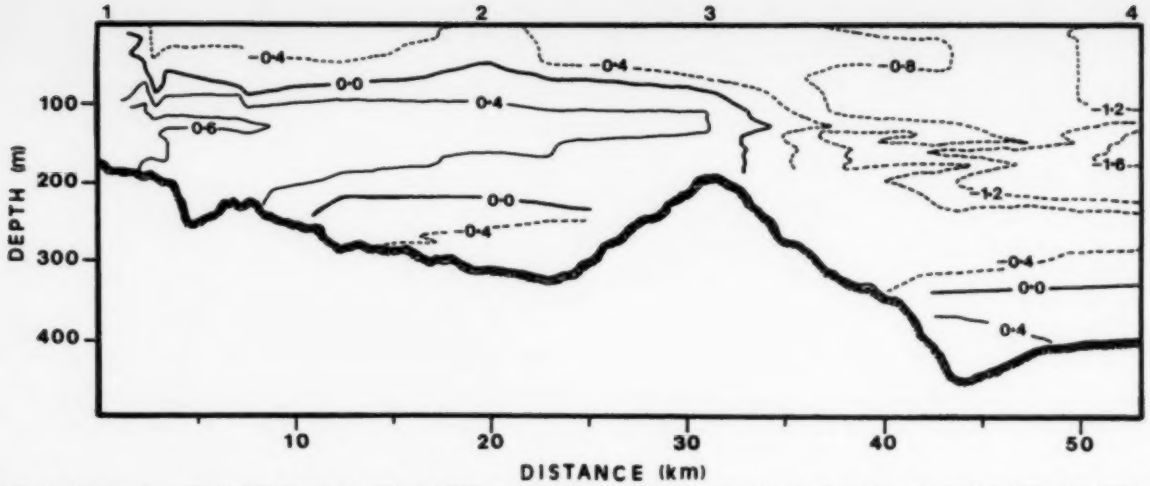


FIG. 4. Temperature section taken at the end of January 1991 along transect line 1,2,3,4, (see Fig. 1) running from the head of Southwest Arm out to the mouth of Trinity Bay, Newfoundland. Solid lines are isotherms >0°C; broken lines are isotherms <0°C.

of warmer water was present in Southwest Arm (Fig. 4). In addition, a pocket of warmer (>0°C) water was recorded deep (>350 m) in Trinity Bay (Fig. 4). By March 1991, however, temperature/depth profiles taken in Hatchet Cove and along a section in Northwest Arm (Wroblewski et al. 1993) revealed uniformly subzero water, with most temperatures at or below −1.0°C. By April 8, 1991, temperature sections showed Southwest and Northwest Arm to be uniformly below 0°C. The cod caught on this date were found in −0.7°C water. These 47 animals had a mean thermal hysteresis level of 0.17 ± 0.01°C (Table 2), suggesting a relatively brief (approximately 19 ± 10 d) exposure to 0°C water (Fig. 3). Fifteen of these fish were identified as belonging to a group of 2690 cod that had been previously caught, tagged, and released in Southwest Arm between January 20 and 27, 1991 as part of the Department of Fisheries and Oceans' (DFO) tagging program. There was no significant difference in antifreeze levels between cod bearing tags (0.19 ± 0.02°C) and the untagged cod (0.15 ± 0.01°C).

Cod caught on May 1, 1992, had high plasma levels of antifreeze with a mean thermal hysteresis value of 0.44°C, indicating exposure to subzero temperatures for approximately 70 ± 10 d (Table 2; Fig. 3). Laboratory experiments have demonstrated that such a high level of antifreeze activity in adult cod is only achieved after long-term exposure to subzero temperatures (Fletcher et al. 1987). The cod caught on May 1 were found at approximately 20 m depth in water that had just warmed to temperatures above 0°C.

Cod caught on May 28 were in the top 40 m in water that had been warming for approximately 4 wk. Their mean thermal hysteresis was 0.25°C (Table 2). Subsequent to sampling, these cod were brought back and held for observation in the laboratory. After 2 mo in seasonally ambient, warm (maximum 9.1, minimum 2.4°C) seawater the remaining cod from this group were sampled again, and all were found to have lost their antifreeze (n = 17; mean thermal hysteresis = 0.063 ± 0.003°C; mean plasma freezing point = −0.69 ± 0.01°C).

On June 18–20, 1992, although surface water temperatures had been above 0°C for almost 50 d, large numbers of cod were caught by otter trawling along the bottom of Southwest Arm in uniformly subzero water. In all cod 40+ cm, thermal hysteresis levels were high (0.43 ± 0.02°C) and plasma freezing points low (−1.34 ± 0.02°C) (Table 2), again indicative of long-term (months) exposure to subzero temperatures (Fig. 3). In cod 30–40 cm in length (n = 13), mean thermal hysteresis was 0.41 ± 0.03°C and mean plasma freezing point was −1.32 ± 0.03°C. There was no significant difference between the <40 and 40+ cm cod in either thermal hysteresis or plasma freezing point ($P > 0.05$ in both cases). None of these values was significantly different from those of the May 1 sample (Table 2) or from maximum values of thermal hysteresis developed in laboratory-held raceway cod continuously exposed to subzero temperatures (Fig. 2).

Between June 29 and 30, 1992, blood samples were taken from 26 cod caught by jigging in Newman Sound, Bonavista Bay. On June 29, 13 cod were caught, seven > 40 cm. While 10 cod had no antifreeze (mean thermal hysteresis = 0.064 ± 0.003°C), three had very high antifreeze levels (length 41, 53, and 83 cm; thermal hysteresis 0.58, 0.28, and 0.63°C, respectively). On June 30, 13 cod were caught (five >40 cm) and none of these 13 fish showed any trace of antifreeze in the plasma (mean thermal hysteresis 0.061 ± 0.003°C). All the cod were caught in approximately 40 m of water at the same site (48.58°N, 53.90°W); however, the temperature/depth profile was considerably different between the two days. On June 29, the bottom temperature was 0.27°C, while the temperature at 30 m was 2.8°C. On June 30, these temperatures were 4.17 and 4.9°C, respectively.

By October 1, 1992, no cod were found in the subzero bottom water of Southwest Arm. Cod were caught only in the warm (>2°C) surface waters. None of these fish had antifreeze in their blood plasma (Table 2).

Between June 2 and 5 of the following year (1993), considerable numbers of cod were caught by otter trawling along Southwest Arm in water at temperatures of −0.9 to −1.2°C. Analysis of antifreeze activity in the plasma of 26 cod (>40 cm) gave mean thermal hysteresis and plasma freezing points of 0.42 ± 0.03°C and −1.35 ± 0.03°C, respectively. These values were consistent with those obtained at

TABLE 2. Levels of thermal hysteresis (antifreeze activity) and plasma freezing points in adult and late juvenile cod (40+ cm) found in Trinity Bay, Newfoundland, between April 1991 and June 1993. Values of thermal hysteresis and plasma freezing points are presented as means ± 1 SE. n = number of fish sampled.

Date	Location	Thermal hysteresis (°C)	Plasma freezing point (°C)
April 8, 1991 (n = 45)	Hatchet Cove, Southwest Arm	0.16 ± 0.01	−1.03 ± 0.01
May 1, 1992 (n = 18)	Resolution Cove, Smith Sound	0.44 ± 0.03	−1.33 ± 0.04
May 28, 1992 (n = 25)	Nut Cove, Smith Sound	0.25 ± 0.02	−1.09 ± 0.02
June 18–20, 1992 (n = 26)	Southwest Arm	0.43 ± 0.02	−1.34 ± 0.02
October 1, 1992 (n = 10)	Southwest Arm	0.07 ± 0.01	−0.90 ± 0.01
June 2–5, 1993 (n = 26)	Southwest Arm	0.42 ± 0.03	−1.35 ± 0.03

the same site the previous year (Table 2), again reflecting long-term exposure to subzero temperatures (Fig. 3).

Discussion

Two principal conclusions can be drawn from this work. First, it demonstrates that the laboratory calibration curve relating plasma antifreeze levels to the length of time spent in subzero waters can be used to deduce the distribution of cod in relation to the temperature field. In other words, antifreeze levels can be used as a physiological time tag to estimate length of continuous exposure to subzero water. However, it must be remembered that in order to draw inferences about the behaviour of cod with respect to temperature, it is necessary to have sufficient information on the temperature field. Thus, this technique is particularly valid when used in a situation such as that described in this paper, where groups of cod were monitored within a well-defined area for which long-term temperature data were available. Predictions of residence time in subzero water can be made with the most confidence when mean antifreeze levels are high, indicating long-term acclimation to 0°C and below. Conclusions as to whether cod make short-term incursions from cold to warm or from warm to cold water cannot be drawn using this technique.

Second, the results clearly demonstrate that some cod overwintering in the Newfoundland inshore area spend considerable lengths of time in subzero waters, many opting to stay at these low temperatures for at least 2 mo after surface waters warm to temperatures above 0°C.

There is considerable literature available on preferred temperatures of cod in the wild. While temperature preference apparently changes somewhat with season, geographic location, and fish size, the majority of favoured ranges are reported to fall between −0.5 and 10°C (Martin and Jean 1964; Beverton and Lee 1965; Templeman and May 1965; Woodhead and Woodhead 1965; Minet and Poulard 1973; Rose and Leggett 1988; Scott and Scott 1988). More specifically, cod of the Northern cod stock have been reported to spend most of their time in water at temperatures between 0 and 5°C, making only short-duration forays into either colder or warmer water, for example, in search of prey organisms (Postolakii 1963; Templeman 1965, 1966; Lear et al. 1986). Thus, it might be expected that when faced with a declining temperature regime such as must be experienced in inshore waters as winter approaches, adult and late juvenile cod would attempt to remain in water close to their preferred temperature, either by leaving inshore areas or, as suggested by Thompson (1943), by inhabiting pockets of warmer water inshore. The data presented in this paper, however, suggest the following pattern of behaviour for cod overwintering in the Trinity Bay area of Newfoundland.

During the summer months (June–August), cod inshore feed pelagically on capelin in surface waters (Templeman 1965; Lilly and Fleming 1981; Lilly and Botta 1984). The elements dictating which fish leave and which stay have yet to be identified; however, as winter approaches, some cod migrate offshore, while others do not. Those remaining inshore stay with their acclimation temperature for as long as possible, and, as the general water temperature in the area declines through 0°C, they produce antifreeze glycoproteins in response to the low temperatures they are experiencing, just as cod held in the laboratory raceway do.

Thermal hysteresis levels in cod caught in April 1991 were consistent with comparatively short-term residence in subzero water (from mid-March, approximately). It seems likely that the 15 cod tagged in Southwest Arm in January 1991 had been resident in the area up to the point where they were caught in April 1991. Further, since there was no significant difference in antifreeze levels between the tagged and untagged cod caught in April, it seems reasonable to assume that they had all been there during the winter. Oceanographic data for the area (Fig. 4) show that a lens of warm water was present in Southwest Arm in January, but was gone by March 13 (Wroblewski et al. 1993). Thus, the data from cod caught in April 1991 suggest that they chose to occupy this warmer water while it was available. As the water cooled, the cod acclimated gradually to the increasingly colder temperatures. By the time water temperatures in the area became uniformly subzero (probably some time in March), they were producing antifreeze glycoproteins and could thus tolerate low temperatures (Fletcher et al. 1987).

Of the 2690 cod tagged in Southwest Arm in January 1991, 812 tagged fish (93% of the total recaptured by April 1, 1992) had been caught by August 31, 1991, less than 30 miles from the tagging location, by the inshore fishery.

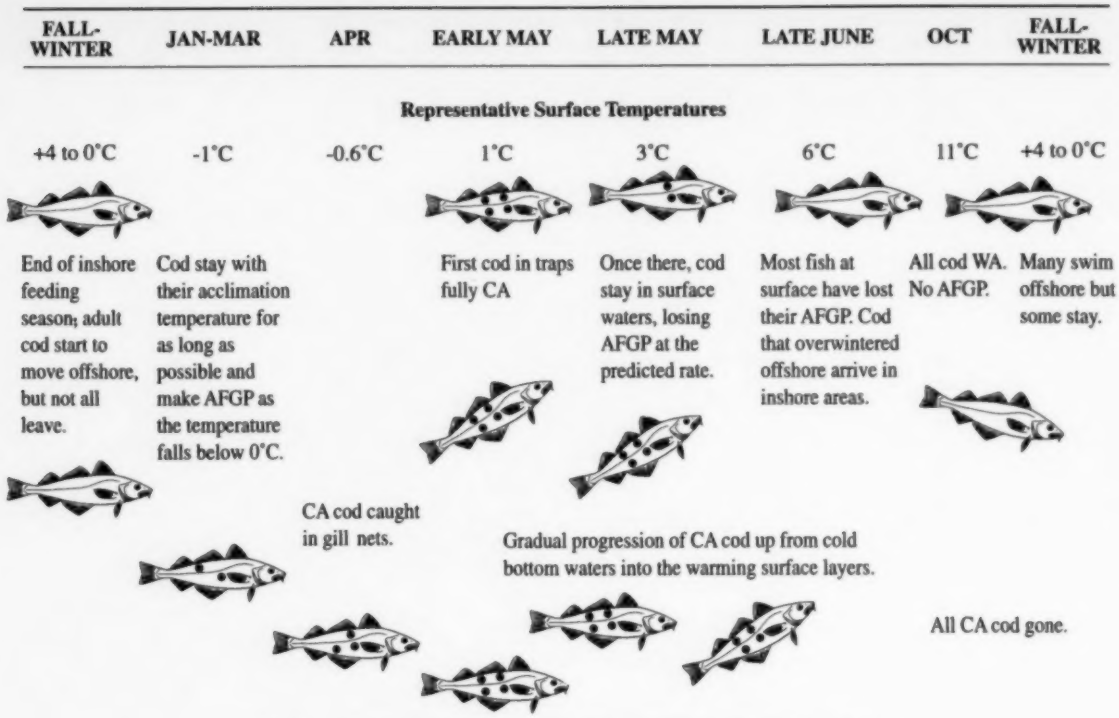

FALL-WINTER
JAN-MAR
APR
EARLY MAY
LATE MAY
LATE JUNE
OCT
FALL-WINTER
Representative Surface Temperatures
+4 to 0°C
-1°C
-0.6°C
1°C
3°C
6°C
11°C
+4 to 0°C
End of inshore feeding season; adult cod start to move offshore, but not all leave.
Cod stay with their acclimation temperature for as long as possible and make AFGP as the temperature falls below 0°C.
First cod in traps fully CA
Once there, cod stay in surface waters, losing AFGP at the predicted rate.
Most fish at surface have lost their AFGP. Cod that overwintered offshore arrive in inshore areas.
All cod WA. No AFGP.
Many swim offshore but some stay.
CA cod caught in gill nets.
Gradual progression of CA cod up from cold bottom waters into the warming surface layers.
All CA cod gone.
Most bottom waters are at subzero temperatures throughout the year

FIG. 5. Data-supported conceptualization of cod distribution in relation to temperature and depth, year-round in Trinity Bay, Newfoundland, as inferred from antifreeze levels and information on temperature and depth of capture obtained between April 1991 and June 1993. AFGP, antifreeze glycoproteins; WA, warm adapted; CA, cold adapted. Degree of cold adaptation (antifreeze level) is represented by solid circles, such that fish with no circles are warm adapted, with no antifreeze; those with two or three circles are either gaining or losing antifreeze; those with four circles are fully adapted to low temperatures, with mean antifreeze levels at maximum.

This suggests either that considerable numbers of cod had remained inshore since January or that the tagged cod had homed back to the tagging area following dispersal. Between January and March 1992, nine of the group tagged inshore in January 1991 were caught in the offshore winter fishery, suggesting that a fish overwintering inshore one year may move offshore to overwinter another year.

On May 1, 1992, cod were caught in surface waters that had just warmed to temperatures above 0°C. Individual thermal hysteresis values in these fish were uniformly high, and the mean level was consistent with mean maximal levels produced by cod held at temperatures below 0°C in the laboratory for approximately 75 d or more (Fig. 2; Table 2). In other words, the wild fish had been in subzero water since at least February 15. During the winter of 1992, the last pocket of water warmer than 0°C in the Random Island region of Trinity Bay was recorded on February 13 (Wroblewski et al. 1993). Thus, oceanographic data corroborate the physiological data and together they strongly suggest that all the adult cod caught in a cod trap on May 1 had been resident in cold inshore water throughout the winter.

In contrast with the cod caught during this study in Trinity Bay in May, a group of 20 adult (>45 cm) cod caught on May 16, 1991, on the northern Grand Banks in water >300 m deep and at temperatures between 1 and 3°C had no trace of antifreeze in the plasma (Howse 1993). Mean thermal hysteresis in these fish was 0.06 ± 0.002°C. The complete absence of plasma antifreeze in all these fish was not unexpected, as they were found in comparatively warm water; however, it further supports the contention that the cod sampled in Trinity Bay on May 1, 1992, had been overwintering at subzero temperatures.

The observations in Trinity Bay during the month of May also provide evidence that inshore overwintering cod become available to the inshore fishery before the arrival of cod from offshore, traditionally estimated to occur after the beginning of June. Solar warming of surface waters to temperatures above 0°C (as happened at the end of April in 1992) may be a signal for cold-adapted fish to start moving into shallow waters where they become available to the trap fishery.

Once antifreeze production ceases, its rate of removal from the plasma is temperature dependent, the biological half-life being approximately 15 d at 5°C, 37 d at 1°C, and almost 100 d at 0°C (Fletcher et al. 1987). Although the May 1 fish were caught at the surface at temperatures >0°C, they had maximal antifreeze levels. This is not surprising because the surface waters only reached temperatures above 0°C at the end of April (Wroblewski et al. 1993). However, by May 28, the mean antifreeze level found in cod caught at the surface had fallen to approximately 57% of that present in the cod sampled on May 1 (an approximate half-life of

34 d). Individual values of thermal hysteresis were consistent with the hypothesis that fish in this sample had been maximally cold adapted but were now losing their antifreeze protection. Using the results for rate of loss of antifreeze against temperature presented by Fletcher et al. (1987), it can be calculated that these fish must have spent the whole 28 d from May 1 to 28 in water temperatures between 1 and 5°C. In other words, rate of loss of antifreeze suggests that once in the warmer surface waters, these cold-adapted cod were staying there rather than returning to the subzero bottom waters in the Random Island area. By the end of summer, previously cold-adapted cod would have lost all their plasma antifreeze while inhabiting the warmer waters near the surface. This contention is supported by the fact that continued exposure to summer temperature conditions (in the laboratory) resulted in a complete loss of antifreeze from the plasma of the cod brought back from Nut Cove. Thus, they exhibited the response typical of all cod held under such conditions in the laboratory during past years (Fletcher et al. 1987).

However, in both 1992 and 1993, cod trawled from the bottom of Southwest Arm in June were found to be maximally cold adapted, suggesting that they had been resident in subzero water for at least 75 d, and presumably for the entire winter (i.e., from some time between January and February). These cod probably represented the remainder of the deepwater group from which the cold-adapted cod caught in April and May originated. It seems likely that from the end of April onward there is a gradual movement of cold-adapted inshore overwintering cod out of the subzero bottom water and into the warming surface layers, possibly in search of food. This movement cannot be motivated simply by the presence of warm water, as some fully cold-adapted cod were still on the bottom in late June, at least 50 d after the surface water warmed above 0°C. The fish caught on June 29–30, 1992, in Newman Sound suggest a possible mechanism for the movement of cold-adapted cod from cold bottom water to warm surface water. Bay-scale oceanographic events bringing cool bottom water and associated cod up into the shallows may play a part in this progression.

By the end of September, trawling along the bottom of Southwest Arm resulted in failure to catch any cod. Cod were only caught at depths <50 m, in temperatures considerably warmer than 0°C, and none of these animals showed any evidence of plasma antifreeze. Either all cold-adapted cod had moved out of Southwest Arm or they had all moved nearer the surface to feed in warmer water and, in the process, had lost all their antifreeze. Of these two alternatives, the latter seems the most likely, particularly because the cod caught in April 1991 were still in the process of becoming cold adapted.

The results of our work have been summarized in a diagram showing cod distribution in the Random Island area of Trinity Bay with respect to temperature, depth, and time using the field data collected between 1991 and 1993 (Fig. 5).

Rose and Leggett (1988) suggested that cod 40+ cm may not be capable of surviving prolonged exposure to temperatures outside the preferred range of −0.5 to 8.5°C, although they found juvenile (15–20 cm) cod living at temperatures near −1°C. During the winter of 1991–92, water temperatures in Northwest and Southwest Arm, Trinity Bay, were consistently low, with the majority of the water column being below −0.6°C (Wroblewski et al. 1993). Indeed, cod were caught in April 1991 at water temperatures between −0.6 and −0.7°C, while in June 1992, cod were trawled from water at temperatures below −1.0°C. The ability of adult cod to survive extreme low temperatures for extended periods in the ocean can, therefore, no longer be in question. However, it is known that when held under the same environmental conditions, antifreeze levels in adults are not high as those found in juvenile cod (Goddard et al. 1992). Thus, at times of extreme low temperature coupled with the presence of ice in the water column, adult cod may exhibit patterns of behaviour that minimize the danger of ice crystal damage, such as occupying deep water and reducing their swimming activity to a minimum.

A further point to note is that mean maximum thermal hysteresis developed by the inshore overwintering cod sampled in the field matched, almost exactly, that developed in winter by cod that had been obtained from the summer (July–August) trap fishery in Conception Bay over a period of 8 yr and overwintered in the laboratory (Table 2; Fig. 2). The July–August trap fishery has always been considered to depend largely on the landward migration of cod that have overwintered offshore on the slopes of the Banks (Templeman 1966; Lear et al. 1986). Thus, it seems likely that many of the cod used to obtain the calibration curve data were part of this landward migration. Therefore, the data suggest that there is little difference in the capacity of offshore and inshore overwintering adult cod to tolerate subzero winter water temperatures, and thus, in terms of low temperature tolerance alone, all adult cod from the Newfoundland/Labrador region appear to have the capacity to overwinter inshore successfully.

An understanding of the physiology of antifreeze production in cod of the "Northern" stocks coupled with extensive oceanographic monitoring of the relatively small study area has allowed us to reach some conclusions on the distribution of cod within the temperature field in Trinity Bay, Newfoundland. With the proviso that calibration curves are obtained for each stock considered, this method may be applicable to investigations of the distribution of other northern populations of cod in relation to low temperature.

Acknowledgements

Our thanks are due to Mr. Austen Oake, National Sea Products Ltd., who first alerted us to the possibility of this fruitful collaboration. We also thank Clyde George, Wayne Edison, and the Captain and crew of M.V. *Shamook* for their contribution to this project. Funding for this research has been provided by OPEN (the Ocean Production Enhancement Network), one of 15 Networks of Centres of Excellence supported by the Government of Canada, and by the Northern Cod Science Program. Funding was provided to J.S.W. by the Natural Sciences and Engineering Research Council of Canada (NSERC), National Sea Products Ltd., and Fishery Products International Ltd. under NSERC's Research Partnerships Program.

References

BEVERTON, R.J.H., AND A.J. LEE. 1965. The influence of hydrographic and other factors on the distribution of cod on the Spitsbergen Shelf. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6: 225–245.

DAVIES, P.L., C.L. HEW, AND G.L. FLETCHER. 1988. Fish antifreeze proteins: physiology and evolutionary biology. Can. J. Zool. 66: 2611–2617.

FISSEL, D.B., AND C.L. TANG. 1991. Response of sea ice drift to wind forcing on the northeast Newfoundland shelf. J. Geophys. Res. 96(C10): 18 397–18 409.

FLETCHER, G.L., M.J. KING, AND M.H. KAO. 1987. Low temperature regulation of antifreeze glycopeptide levels in Atlantic cod (*Gadus morhua*). Can. J. Zool. 65: 227–233.

GODDARD, S.V., M.H. KAO, AND G.L. FLETCHER. 1992. Antifreeze production, freeze resistance, and overwintering of juvenile northern Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 49: 516–522.

HEW, C.L., D. SLAUGHTER, G.L. FLETCHER, AND S.B. JOSHI. 1981. Antifreeze glycoproteins in the plasma of Newfoundland Atlantic cod (*Gadus morhua*). Can. J. Zool. 59: 2186–2192.

HOWSE, K.A. 1993. A modified migration model for Atlantic cod, *Gadus morhua*, off the northeast coast of Newfoundland. M.Sc. thesis, Memorial University of Newfoundland, St. John's, Nfld.

KAO, M.H., AND G.L. FLETCHER. 1988. Juvenile Atlantic cod (*Gadus morhua*) can be more freeze resistant that adults. Can. J. Fish. Aquat. Sci. 45: 902–905.

KAO, M.H., G.L. FLETCHER, N.C. WANG, AND C.L. HEW. 1986. The relationship between molecular weight and antifreeze polypeptide activity in marine fish. Can. J. Zool. 64: 578–582.

LEAR, W.H., J.W. BAIRD, J.C. RICE, J.E. CARSCADDEN, G.R. LILLY, AND S.A. AKENHEAD. 1986. An examination of factors affecting catch in the inshore cod fishery of Labrador and eastern Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1469: 71 p.

LEAR, W.H., AND J.M. GREEN. 1984. Migration of the "northern" Atlantic cod and the mechanisms involved, p. 309–315. *In* J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill [ed.] Mechanisms of migration in fishes. Plenum Press, New York, N.Y.

LILLY, G.R., AND J.R. BOTTA. 1984. Food of Atlantic cod (*Gadus morhua* L.) near Bonavista, Newfoundland in 1983. NAFO SCR Doc. 84/VI/51, Ser. N. N838: 8 p.

LILLY, G.R., AND A.M. FLEMING. 1981. Size relationships in predation by Atlantic cod, *Gadus morhua*, on capelin, *Mallotus villosus*, and sand lance, *Ammodytes dubius*, in the Newfoundland area. NAFO Sci. Counc. Stud. No. 1: 41–45.

MARTIN, W.R., AND Y. JEAN. 1964. Winter cod taggings off Cape Breton and on offshore Nova Scotia banks, 1959–62. J. Fish. Res. Board Can. 21: 215–238.

MINET, J.P., AND J.C. POULARD. 1973. Winter distribution of cod (*Gadus morhua* L.) off the southwest coast of Newfoundland (ICNAF Div. 4R) in relation to water temperature. ICNAF Res. Doc. 73/35: 12 p.

NEGULESCU, P.A., B. RUBINSKY, G.L. FLETCHER, AND T.E. MACHEN. 1992. Fish antifreeze proteins block Ca entry into rabbit parietal cells. Am. J. Physiol. 263 (Cell Physiol. 32): C1310–C1313.

PETRIE, B., S. AKENHEAD, J. LAZIER, AND J. LODER. 1988. The cold intermediate layer on the Labrador and northeast Newfoundland shelves, 1978–86. NAFO Sci. Counc. Stud. 12: 57–69.

POSTOLAKII, A.I. 1963. Biology and fishing of Labrador and Newfoundland cod. Tr. PINRO: 3–43. (Fish. Res. Board Can. 1972. Transl. Ser. 2151: 44 p.)

ROSE, G.A., AND W.C. LEGGETT. 1988. Atmosphere–ocean coupling and Atlantic cod migrations: effects of wind-forced variations in sea temperatures and currents on nearshore distributions and catch rates of *Gadus morhua*. Can. J. Fish. Aquat. Sci. 45: 1234–1243.

RUBINSKY, B., A. ARAV, AND G.L. FLETCHER. 1991. Hypothermic protection — a fundamental property of "antifreeze" proteins. Biochem. Biophys. Res. Commun. 180: 566–571.

RUBINSKY, B., A. ARAV, M. MATTIOLI, AND A.L. DEVRIES. 1990. The effect of antifreeze glycoproteins on membrane potential changes at hypothermic temperatures. Biochem. Biophys. Res. Commun. 173: 1369–1374.

SCOTT, W.B., AND M.G. SCOTT. 1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219: 731 p.

SOKAL, R., AND F.J. ROHLF. 1981. Biometry. W.H. Freeman & Co., New York, N.Y. 859 p.

SYMONDS, G. 1986. Seasonal ice extent on the northeast Newfoundland shelf. J. Geophys. Res. 91(C9): 10 718–10 724.

TAGGART, C.T., AND K.T. FRANK. 1987. Coastal upwelling and *Oikopleura* occurrence ("slub"): a model and potential application to inshore fisheries. Can. J. Fish. Aquat. Sci. 44: 1729–1736.

TEMPLEMAN, W. 1965. Some instances of cod and haddock behaviour and concentrations in the Newfoundland and Labrador areas in relation to food. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6: 449–461.

TEMPLEMAN, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. 154: 170 p.

TEMPLEMAN, W., AND A.M. FLEMING. 1965. Cod and low temperature in St. Mary's Bay, Newfoundland. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6: 131–135.

TEMPLEMAN, W., AND A.W. MAY. 1965. Research vessel catches of cod in the Hamilton Inlet Bank area in relation to depth and temperature. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6: 149–165.

THOMPSON, H. 1943. A biological and economic study of cod (*Gadus callarias*, L.) in the Newfoundland area including Labrador. Nfld. Gov. Dep. Nat. Resour., St. John's, Res. Bull. (Fish.) 14: 160 p.

WOODHEAD, P.M.J., AND A.D. WOODHEAD. 1965. Seasonal changes in the physiology of the Barents Sea cod *Gadus morhua* L., in relation to its environment. II. Physiological reactions to low temperatures. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6: 717–734.

WROBLEWSKI, J.S., W.L. BAILEY, AND K.A. HOWSE. 1994. Observations of adult Atlantic cod (*Gadus morhua*) overwintering in nearshore waters of Trinity Bay, Newfoundland. Can. J. Fish. Aquat. Sci. 51: 142–150.

WROBLEWSKI, J.S., A. COLLIER, AND W. BAILEY. 1993. Ocean temperatures in the Random Island region of Trinity Bay, 1991–1992. The NSERC/Fishery Products International/National Sea Products Chair in Fisheries Oceanography, Data Rep. No. 1. Memorial University, St. John's, Nfld. 48 p.

A Relationship between Fraser River Discharge and Interannual Production of Pacific Salmon (*Oncorhynchus* spp.) and Pacific herring (*Clupea pallasi*) in the Strait of Georgia

Richard J. Beamish, Chrys-Ellen M. Neville, and Barbara L. Thomson

Department of Fisheries and Oceans, Pacific Biological Station, Hammond Bay Rd., Nanaimo, BC V9R 5K6, Canada

and Paul J. Harrison and Mike St. John

Department of Oceanography, University of British Columbia, 6270 University Blvd., Vancouver, BC V6T 1W5, Canada

Beamish, R.J., C.-E.M. Neville, B.L. Thomson, P.J. Harrison, and M. St. John. 1994. A relationship between Fraser River discharge and interannual production of Pacific salmon (*Oncorhynchus* spp.) and Pacific herring (*Clupea pallasi*) in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 51: 2843–2855.

We identified years of anomalously high and low discharge from the Fraser River and compared these years with indices of anomalously high and low production of Pacific salmon (*Oncorhynchus* spp.) and Pacific herring (*Clupea pallasi*). For chinook (*O. tshawytscha*) and coho salmon (*O. kisutch*), we found that brood years that went to sea in a year when the Fraser River discharge was very high compared with the previous year virtually never had an index of production that was higher than the previous year. Similarly, brood years that went to sea in a year when the Fraser River discharge was very low compared with the previous year almost never had an index of productivity that was lower than the previous year. The analysis identified a weaker association between extreme discharge anomalies and chum salmon (*O. keta*) production. A close association was not found between extreme discharge anomalies and pink salmon (*O. gorbuscha*), sockeye salmon (*O. nerka*), or herring production. The relationships identify a connection between annual fluctuations in river flow and production of some marine fishes and may be of use in forecasting abundance changes.

Nous avons repéré des années où le débit du Fraser était anormalement élevé ou bas et mis en relation ces années avec des indices de production anormalement élevés ou bas chez les saumons du Pacifique (*Oncorhynchus* spp.) et le hareng du Pacifique *Clupea pallasi*. Dans les cas du quinnat (*O. tshawytscha*) et du coho (*O. kisutch*), nous avons observé que l'indice de production des contingents qui effectuaient leur avalaison dans une année où le débit du Fraser était très élevé par rapport à celui de l'année précédente n'était pour ainsi dire jamais supérieur à l'indice des contingents de l'année précédente. De même, l'indice de production des contingents qui effectuaient leur avalaison dans une année où le débit du Fraser était très bas par rapport à celui de l'année précédente n'était pour ainsi dire jamais inférieur à l'indice des contingents de l'année précédente. La corrélation entre les débits extrêmes et la production chez le kéta (*O. keta*) était plus faible. Enfin, on n'a pas observé de corrélation serrée entre ces deux paramètres dans les cas du saumon rose (*O. gorbuscha*), du saumon rouge (*O. nerka*)) et du hareng. Ces analyses ont permis d'établir l'existence d'une relation entre les fluctuations interannuelles du débit et la productivité de certaines espèces de poissons marins, relation qui pourrait être prise en considération dans la prévision des variations d'abondance.

Received October 18, 1993
Accepted May 30, 1994
(J12127)

Reçu le 18 octobre 1993
Accepté le 30 mai 1994

The Strait of Georgia, located between Vancouver Island and the British Columbia mainland (Fig. 1), is an important marine ecosystem on Canada's west coast and one of the most important salmon-producing areas in the Pacific Ocean. There are five species of Pacific salmon that are resident in or move through the Strait of Georgia: pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*), coho (*O. kisutch*), and chinook (*O. tshawytscha*). Most of the production of these five species comes from the Fraser River which produces more Pacific salmon than any other river in British Columbia. For the 5-yr period 1986–90, approximately 32% of the average total Canadian catch of Pacific salmon or approximately 41% of the total catch in a year of Fraser River pink salmon returns originated from the Fraser River.

The Strait of Georgia is 220 km long, 33 km wide, has a surface area of about 6900 km^2, an average depth of 155 m, and a maximum depth of 420 m (Waldichuk 1957). It is connected to the Pacific Ocean in the north by Johnstone Strait and in the south by Juan de Fuca Strait. Approximately 80% of the fresh water entering the Strait of Georgia comes from the Fraser River (Waldichuk 1957). The total volume of the freshwater discharge reduces the surface salinity, and because of the reduced salinity and the semienclosed nature of the strait, it could be considered a large estuary according to the definition of Pritchard (1967). Discharge from the Fraser River establishes the estuarine circulation of less-dense surface water flowing out of the strait, compensated by deep water flowing into the strait from offshore. This deep water enters through Juan de Fuca Strait (Thomson 1981) and the

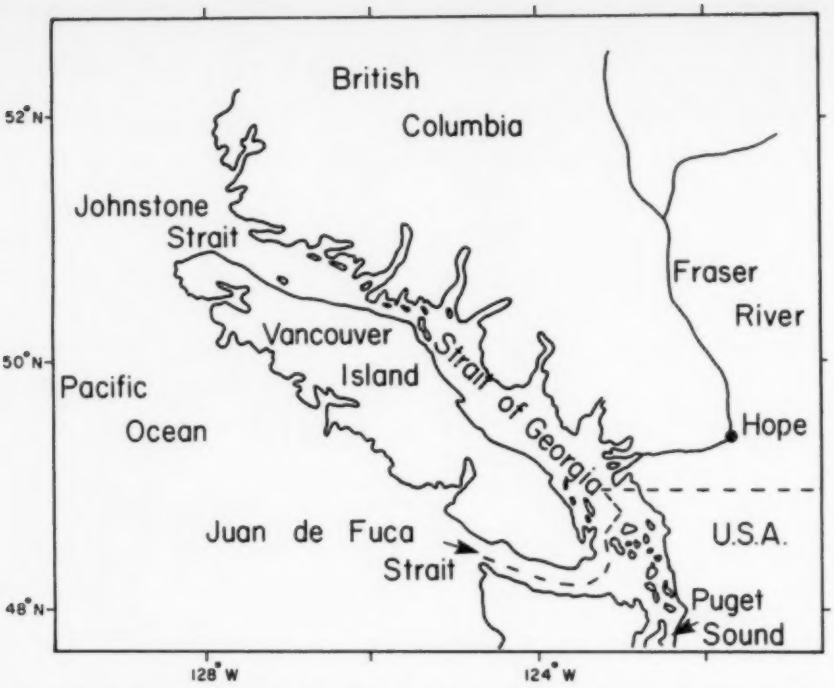


FIG. 1. Study area, showing the Strait of Georgia, lower Fraser River, and other locations mentioned in the text.

nutrient-rich waters are eventually entrained into the surface waters (Harrison et al. 1983; St. John et al. 1992). The estuarine circulation, therefore, has a major impact on the marine food production system in the Strait of Georgia. It follows that Fraser River flows must be considered to be linked to the marine food production system in the Strait of Georgia. Assuming that the early marine mortality of salmon is directly or indirectly related to the availability of food, the flow from the Fraser River could be associated with the marine mortality of salmon. Because most marine mortality of salmon occurs shortly after the smolts enter salt water (Parker 1968; Bax 1983), there might be a relationship between Fraser River flows and salmon year-class strength (termed brood year when referring to salmon).

The highest recorded discharge from the Fraser River was in 1976, followed by a very low discharge in 1977. In 1977, chinook and coho salmon entering the Strait of Georgia had exceptionally high survival resulting in large catches from these year classes (Beamish 1993). The exceptional production in 1977 lead to our hypothesis that the pattern of Fraser River discharge might be related to trends in fish production within the strait.

In this study, we examined the interannual relationships between annual changes in Pacific salmon and Pacific herring (*Clupea pallasi*) production and annual changes in Fraser River discharge. We compared annual discharge with annual fish production using the data series and residuals from smoothed trends in these series. There was no apparent relationship between discharge and long-term abundance trends except for one coho catch data series. We have not included these results in this report because the examination of long-term trends in abundance is confounded by the additions of hatchery-reared salmon and regulation changes. We expect to be able to report on the relationship between long-term abundance trends and annual discharge trends in a separate publication. In this paper we focus on the interannual relationship between discharge change and indices of fish productivity changes. We included five salmon species because they all spend time in the Strait of Georgia, but we expected that a relationship would be most evident for chinook and coho because they spend more time in the strait than the other species. We included herring because earlier studies (Stocker et al. 1985) identified Fraser River discharge as one environmental variable that was associated with year-class strength.

Data and Methods

Data Analysis

We compared change in Fraser River discharge rate with our indices of abundance or survival for Pacific salmon and herring. We looked at production anomalies over short intervals to minimize the impact of factors such as regulation changes or natural changes in the ecosystem that changed the relativity of values in the time series. To test the hypothesis that there was no relationship between anomalous discharge rate and fish production in the Strait of Georgia, we initially looked at anomalies to a 2-yr average for each value in the fish production and discharge data series. We observed that a 2-yr anomaly provided a good estimate of years of extreme change in discharge. However, for the fish production time series, anomalies to a 3-yr average are more representative of positive or negative changes in production. So, for this paper, we used both 2- and 3-yr anomalies.

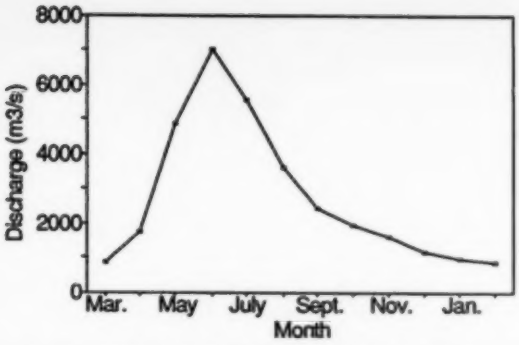


FIG. 2. Average daily discharge rate of the Fraser River averaged for each month from 1960 to 1992. March is the month with the lowest average daily discharge and June has the highest discharge. Discharge reaches a maximum quickly during May and June.

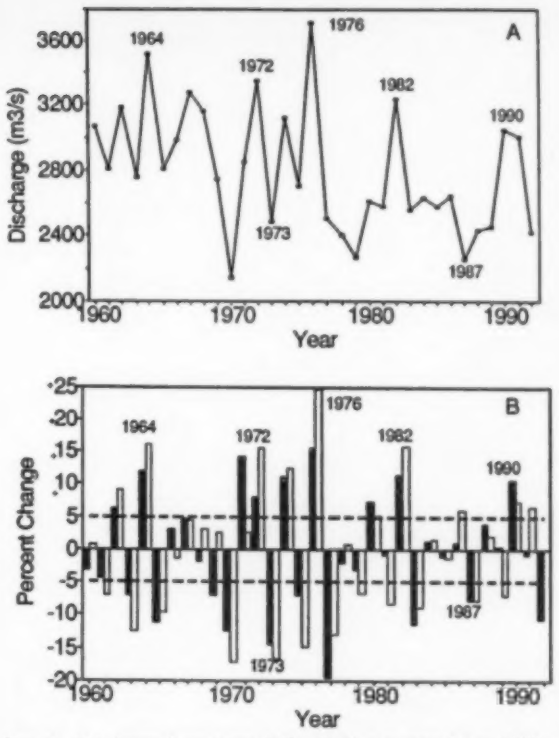


FIG. 3. (A) Annual average daily discharge rate from 1960 to 1992 showing the variation in annual discharge. For reference, some of the extreme years in discharge are identified. The highest average daily discharge rate occurred in 1976. Note that the pattern of discharge changes and appears to decline after 1976. (B) Changes in discharge expressed as a percent change from the previous year (2-yr changes) and previous and following years (3-yr changes). Years of anomalous high discharge were chosen to be those years greater than 5%; years of anomalous low discharge were those less than 5% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

The fish production time series were selected based on their availability, length, and because there was a reasonable probability that the series represented an index of year-class abundance or survival. Our indices of abundance may not be directly proportional to changes in population size, but we speculated that an increase or a decrease in abundance of salmon would be reflected in the catches in unregulated fisheries or in quota revisions in regulated fisheries. We expected that some errors and approximations were present in the time series, but these were likely to occur in only a short portion of the series. Because the time series were relatively long, we expected that an association of natural, interannual abundance changes with interannual changes in discharge might be apparent despite some errors in the data series. All abundance indices were lagged to match the year salmon entered the Strait of Georgia or the year herring spawned. Except for Pacific herring, chum salmon, and the hatchery survival data series for chinook and coho salmon, we started our time series in 1960 when recreational fishing data for coho were first available. Data were available for some fisheries a few years earlier, but to minimize data errors associated with some of the early data, and to ensure that we compared discharge and production over a long enough period, we chose to start all salmon data series in 1960. The Pacific herring abundance index started in 1975, chum salmon abundance estimates in 1965, and the hatchery survival data in 1973, as will be explained subsequently.

We calculated the 2- and 3-yr anomalies in each time series by comparing values in one year (1) with the average of that year and the preceding year and (2) with the average of the one year and the preceding and following years and expressing this difference as a percentage of the 2- or 3-yr average as follows:

$$(1)\quad Z_i = \left(X_i \left(\sum_{j=-1}^{0} X_{i+j}/2 \right) \right) \Big/ \left(\sum_{j=-1}^{0} X_{i+j}/2 \right) \times 100$$

$$(2)\quad Z_i = \left(X_i \left(\sum_{j=-1}^{1} X_{i+j}/3 \right) \right) \Big/ \left(\sum_{j=-1}^{1} X_{i+j}/3 \right) \times 100$$

where Z_i = is the percent change in year i and X_i is the value in the current year. Depending on the data series, we chose a value of above or below between a 5 and 20% change as an extreme anomaly.

We tested the hypothesis that there was no relationship between changes in Fraser River discharge and the production anomalies using a chi-square (χ^2) test (Press et al. 1986). Each chi-square table compared anomalies of high discharge and poor production, average discharge and poor production, low discharge and poor production, high discharge and good production, average discharge and good production, and low discharge and good production. We excluded years of average fish production because we were comparing anomalous fish production with Fraser River discharge.

Fraser River Discharge

Freshwater discharge from the Fraser River results mostly from snow melting in the mountains in the drainage area. Most melting occurs in the spring (Moore 1991), resulting in a pattern of annual discharge that is low early in the year and reaches a maximum in June (Fig. 2). The discharge rate is measured daily at Hope (Fig. 1) and measurements were

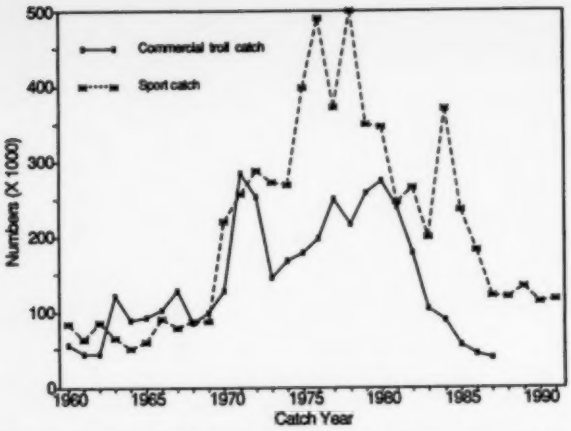


FIG. 4. Number of chinook salmon caught in the commercial troll and sport fisheries in the Strait of Georgia. In the early 1970s, the sport catch increased and exceeded the commercial troll catch, but the general trends in abundance were similar. In the 1980s, catches in both fisheries declined.

published by Environment Canada (1990). We used an average of the 12 average monthly discharge rates as an index of average annual discharge. We used the 12-mo period between April 1 and March 31 of the following year. This provided an index of the total discharge between the lowest values in the annual cycle (Fig. 3A).

Chinook Salmon

Chinook salmon that enter the Strait of Georgia are produced in approximately 75 rivers that flow directly or indirectly into the strait (Argue et al. 1983) and in almost 20 Canadian hatcheries. Most chinook salmon spawn in the fall and their progeny enter salt water in the late spring of the following year. In general, chinook salmon return to spawn in their natal streams between their second and fifth year of ocean life (Healey 1991). During the period of ocean residence, chinook salmon originating from rivers and hatcheries around the Strait of Georgia may remain in the strait or may move offshore. The commercial and sport fisheries in the strait catch chinook produced from rivers and hatcheries around the strait, as well as chinook produced in rivers and hatcheries in Puget Sound in the United States (Argue et al. 1983). The commercial and sport catch of chinook salmon is available through the Department of Fisheries and Oceans data bases (Kuhn et al. 1988; Holmes and Whitfield 1991).

Chinook salmon from any particular brood year can appear in the catch over a number of years, and it has been shown that the relative abundance of the age-2 fish (i.e., 2 yr after spawning or one winter annulus) is indicative of the relative survival of chinook salmon produced in hatcheries (Fraser et al. 1983). Thus, it is possible that the abundance of age-2 fish is also an index of year-class strength. We used catch and age composition data to calculate an index that reflected the abundance of age-2 fish.

The trends in the catch of chinook in the commercial and sport fisheries were similar over the time series, except, beginning in the mid-1970s, sport catches exceeded commercial catches (Fig. 4). Before 1983, estimates of age composition in the sport fishery were not available, but estimates

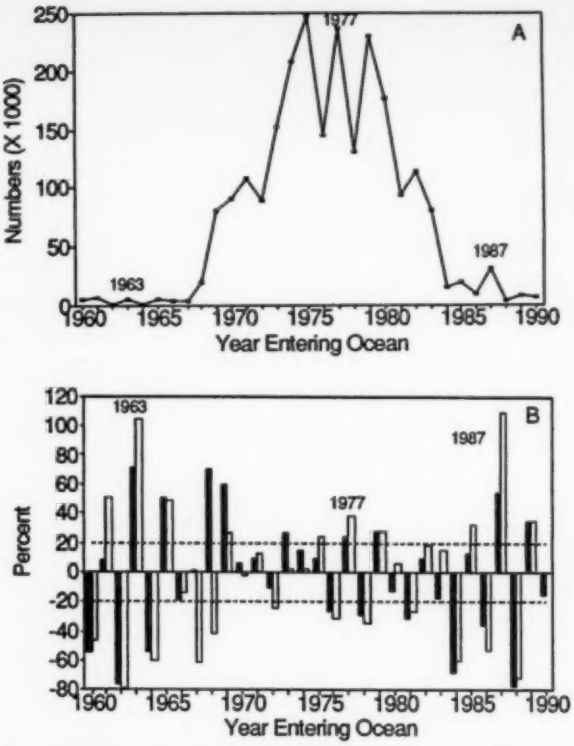


FIG. 5. (A) Two-year-old index of chinook salmon caught in the Strait of Georgia sport fishery. The numbers are related to the year that the smolts entered the ocean. (B) The data in Fig. 5A expressed as a percent change. Years of anamalous good production were greater than 20%; years of anomalous low production were less than 20% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

of the catch of age-2 or "jack" chinook salmon in the commercial fisheries were (B.E. Riddell, Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, B.C., personal communication). We used the proportion of "jack" chinook salmon in the commercial fishery as an index of the percentage of age-2 chinook in the sport fishery for the period 1960–1982. For the period 1983–1990, the estimated proportion of age-2 chinook in the sport fishery was taken from the age composition estimates of fish from the sport creel survey (Collicutt and Shardlow 1992). The age-2 index, therefore, approximates the percentage of age-2 fish caught in the sport fishery and is expressed as numbers of chinook caught (Fig. 5A). Due to the potential differences in exploitation patterns and regulatory mechanisms between the sport and commercial fisheries and changes within the fisheries themselves, the commercial data may not accurately estimate the proportion of age-2 fish caught in the sport fishery. However, in using the calculated index, we assumed that the catches from both fisheries will reflect large interannual changes in the abundance of age-2 chinook and that our index may capture these changes.

We also used the total catch of chinook in the sport fishery in the strait as an index of year-class strength. The sport fishery operates throughout the year, and until increased size limits were introduced beginning in 1981, a strong chinook

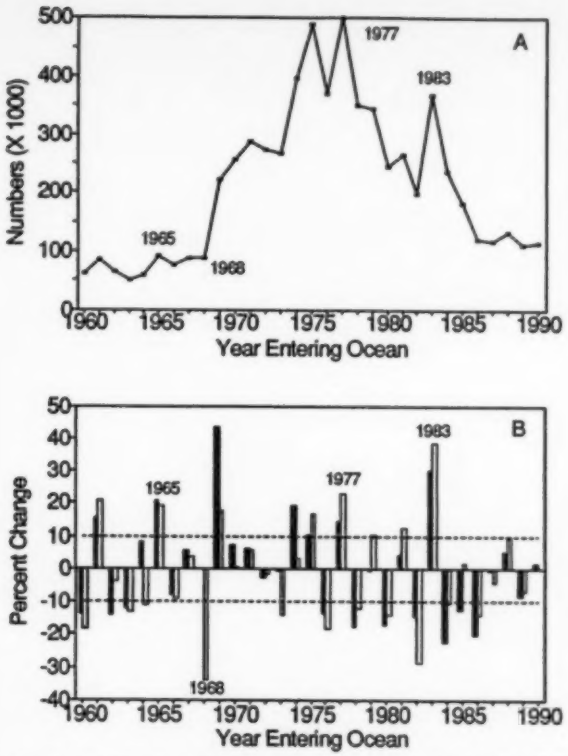


FIG. 6. (A) Number of chinook salmon caught in the Strait of Georgia sport fishery. The numbers are related to the year that the smolts entered the ocean. (B) The data in Fig. 6A expressed as a percent change. Years of anomalous good production were greater than 10%; years of anomalous low production were less than 10% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

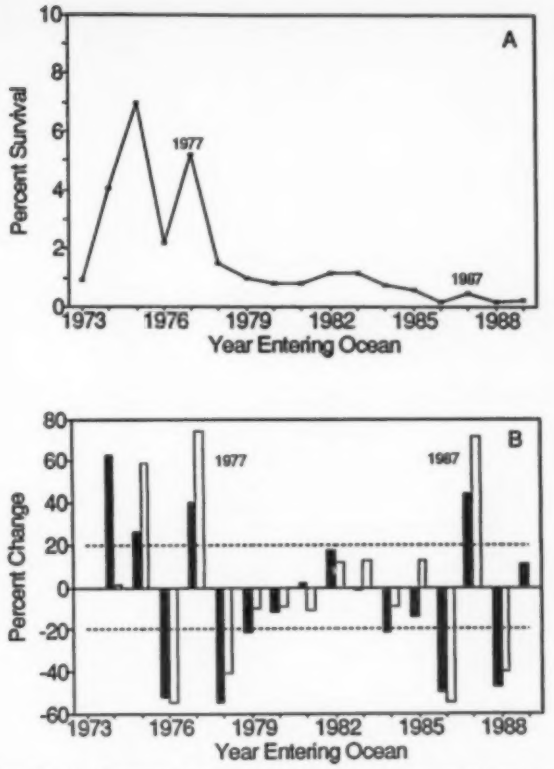


FIG. 7. (A) Percent survival of chinook salmon produced in hatcheries in the Strait of Georgia and the Fraser River. Percent survival for each brood year is related to the year that the brood year entered the ocean. Over the time series, hatchery survival trends increased and then decreased. (B) The data in Fig. 7A expressed as a percent change. Years of anomalous good production were greater than 20%; years of anomalous low production were less than 20% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

year class would be expected to be identifiable in the catch in its second marine year (Fig. 6A). We did not expect the total sport catch to be as representative of brood-year strength as the age-2 index, because the chinook caught in the fishery were from multiple age classes. Nevertheless, it was possible that above or below-average brood-year strength might be detectable in the sport catch. For this analysis, we assumed that the fish were caught at age 3.

The third data series used to represent chinook production was the percent survival of chinook salmon from hatcheries (Fig. 7A). Hatchery survival estimates, based on returns of salmon marked with coded-wire tags, were available from 1973 until the most recent complete brood-year returns in 1988 (Kuhn et al. 1988).

Coho Salmon

Coho salmon are common in many of the streams and rivers that flow into the strait (Argue et al. 1983) and are reared in approximately 20 Canadian hatcheries. Coho salmon spawn in fresh water in the fall and the eggs hatch in the following spring. Most young coho spend 1 yr in fresh water before entering the ocean (Sandercock 1991). During the period of ocean residence, coho may remain in the strait or they may move offshore. Most coho salmon return to their natal streams in their second year of ocean life (Sandercock 1991).

The commercial and sport catches of coho salmon in the Strait of Georgia are available through the records of the Department of Fisheries and Oceans (Holmes and Whitfield 1991; Collicutt and Shardlow 1992). Beginning in the late 1960s, the sport catch of coho greatly exceeded the commercial catch, but the trends in catch were similar (Fig. 8, 9A, 10A). Because the coho catch is virtually from one brood year, we used data bases from both the sport and commercial fisheries as an index of production.

The third coho salmon data series was the percent survival of hatchery-reared coho beginning in 1973 (Fig. 11A). In the 1970s and 1980s, hatcheries located around the Strait of Georgia produced coho that were released into the strait. Estimates of the numbers of smolts released by hatcheries into the Strait of Georgia and the Fraser River and the return of adults from these releases were used to calculate hatchery survival (Kuhn et al. 1988).

Pink, Chum, and Sockeye Salmon

Pink, chum, and sockeye salmon produced in the Fraser River are thought to reside in the strait for only a few months. We used salmon production data from the Fraser

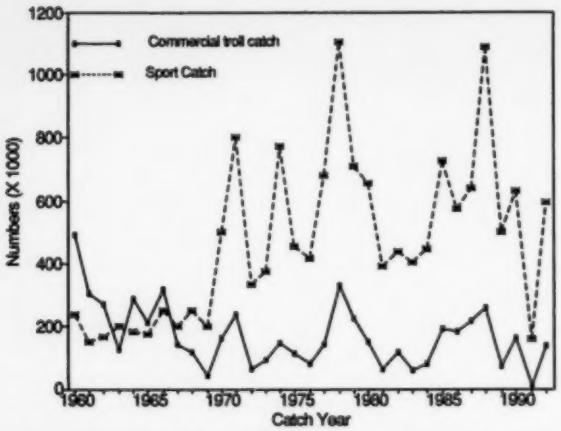


FIG. 8. Number of coho salmon caught in the commercial troll and sport fisheries in the Strait of Georgia. Beginning in the early 1970s, the sport catch exceeded the commercial troll catch. The total catch in the sport fishery fluctuated as a result of changes in effort and fish abundance but not as a result of direct quota regulation. In 1991, the coho catch in both fisheries declined dramatically and was the lowest in the data series.

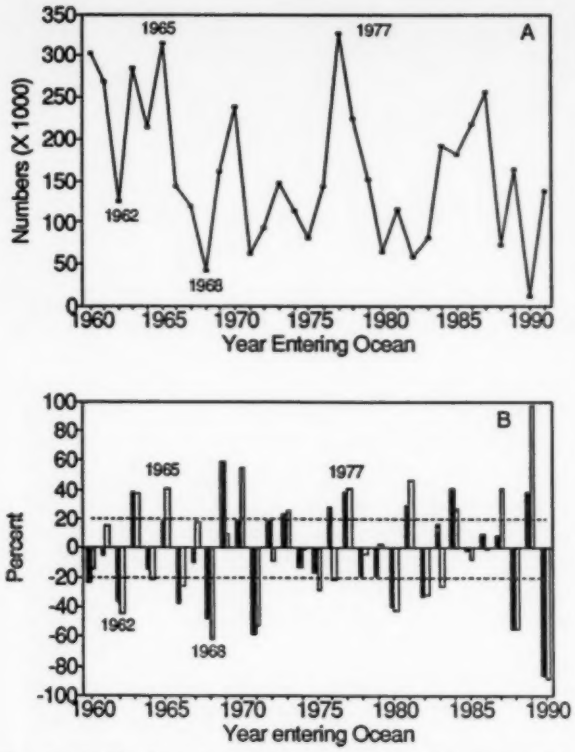


FIG. 9. (A) Number of coho salmon caught in the commercial troll fishery in the Strait of Georgia. The numbers are related to the year that the smolts entered the ocean. Catch year would be 1 yr later and brood year would be 2 yr earlier. The catch in 1978 of coho entering the ocean in 1977 is the highest in the time series. (B) The data in Fig. 9A expressed as a percent change. Years of anomalous good production were greater than 20%; years of anomalous low production were less than 20% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

River because virtually all of the pink and sockeye salmon and many of the chum salmon that move through the strait are from the Fraser River (Healey 1980).

Chum salmon spawn in the fall and the eggs hatch in the following spring. Chum salmon from the Fraser River move into the Strait of Georgia from April to May (Healey 1980). They are reported to remain in the strait until July, when they migrate into the northern North Pacific Ocean (Healey 1980). We determined brood-year strength for chum salmon by partitioning estimates of the annual catch and escapement for Fraser River stocks, available for the period 1965–1987 (Beacham and Starr 1982; M. Joyce, Fraser River Division, Department of Fisheries and Oceans, personal communication), into age groups using the percentage age composition (age 2 = 28.1%, age 3 = 61.4%, age 4 = 10.5%) determined by Beacham and Murray (1987). We then assigned the appropriate catch and escapement to the appropriate brood year to produce an index of brood-year strength (Fig. 12A) that was then used to identify high and low years of production and test significance as was done for the other salmon (Fig. 12B).

Pink salmon spawn in the fall, and the fry that hatch in the following spring begin their downstream migration immediately after emerging from the gravel (Neave 1966). The young pink salmon migrate into the strait during March and April, and by July, virtually all pink salmon have left the strait (Healey 1980). Almost all pink salmon from the Fraser River spawn in odd-numbered years and the fry enter the Strait of Georgia in even-numbered years (Neave 1966). We used estimates of catch and escapement produced by the Pacific Salmon Commission (PSC 1990) as an index of brood-year strength (Fig 13A).

Sockeye salmon in the Fraser River spawn in the fall, and the fry that emerge from the gravel early in the year move into lakes where most remain for 1 yr before going to sea as smolts. The smolts move into the Strait of Georgia toward the last 2 wk of April, and by the end of May, most have left the strait (Groot and Cooke 1987). The sockeye smolts move northward, remaining in the strait for about 1 mo. This is the shortest period of residence in the strait of any of the five species of Pacific salmon. Almost all (90%) of the sockeye salmon from the Fraser River spend 2 yr in the ocean before they return to spawn (Vernon 1982).

Most of the stocks of sockeye salmon from the Fraser River are characterized by 4-yr cyclic abundance changes (Fig. 14A). The largest of the lines or years that make up a cycle is dominated by the Adams River stock that returned to spawn in 1982, 1986, 1990, etc. There is no consensus about the mechanism responsible for the cycles, but their existence requires that production from each of the four years in the cycle be compared separately. Catch and escapement data were obtained from the Pacific Salmon Commission (PSC 1986–1989) and International Pacific Salmon Fisheries Commission (IPSFC 1965–1985) and separated into the 4-yr cycles (Fig. 14A). Within each cycle, the relative production of each year or line was compared with the same line in the previous cycle (Fig. 14B).

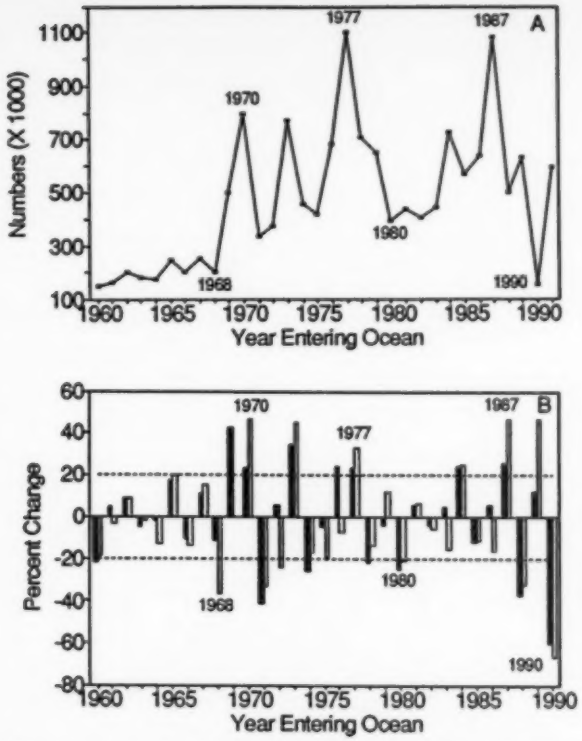


FIG. 10. (A) Number of coho salmon caught in the sport fishery in the Strait of Georgia. The numbers are related to the year that the smolts entered the ocean. Catch year would be 1 yr later and brood year would be 2 yr earlier. Note in this figure and in Fig. 9 the very low catch in 1991 of coho that went to sea in 1990 and the high catch in 1978 of coho that went to sea in 1977. (B) The data in Fig. 10A expressed as a percent change. Years of anomalous good production were greater than 20%; years of anomalous low production were less than 20% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

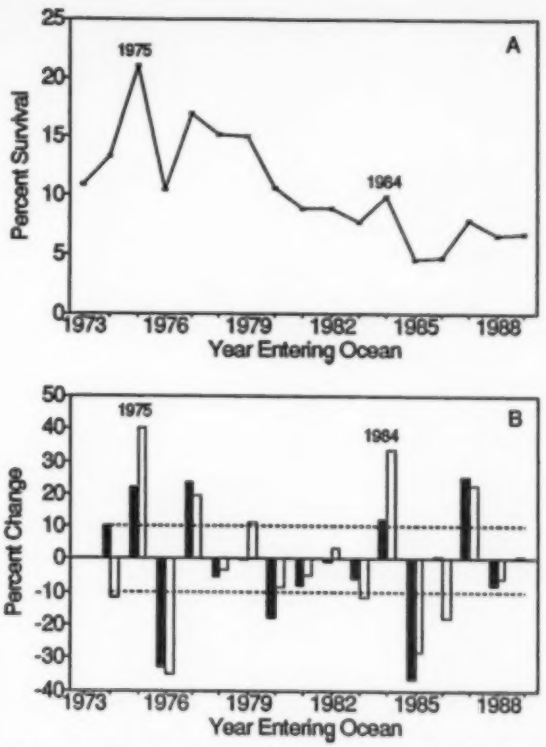


FIG. 11. (A) Percent survival of coho salmon produced in hatcheries in the Strait of Georgia and the Fraser River. Percent survival for each brood year is related to the year that the brood year entered the ocean. There is a declining trend in survival, but an increasing number of smolts were released until the mid-1980s (Cross et al. 1991). There is not as much interannual variation as occurred in the catch data. (B) The data in Fig. 11A expressed as a percent change. Years of anomalous good production were greater than 10%; years of anomalous low production were less than 10% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

Pacific Herring

Pacific herring stocks in the Strait of Georgia provide food for salmon and other predators, as well as sustaining an important commercial fishery. There is a small resident population and a larger migratory population that moves into the strait in the fall and spawns in the following winter (Hourston and Haegele 1980). The juvenile herring remain in the strait for over a year, migrating offshore in the following summer.

The Pacific herring fishery was the largest fishery in British Columbia from the late 1940s to the mid-1960s with catches in the 1950s and 1960s of approximately 200 000 t (Hourston and Haegele 1980). However, the large catches of the early 1960s (up to 260 000 t) could not be sustained and the fishery was shut down in 1968. The fishery started again in 1971 as a roe fishery and currently harvests about 35 000 to 40 000 t. An index of the age-2+ biomass has been produced starting in 1952 (Schweigert et al. 1993), but because of sampling problems in the late 1960s and early 1970s associated with the closure of the fishery, the reconstructions of year classes for this period may only approximate the actual population structure (V. Haist, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C., personal communication) Thus, we arbitrarily started our data series in 1975 (Fig. 15A). We identified strong and weak year classes using the age-2+ biomass in Schweigert et al. (1993) for all Strait of Georgia Pacific herring stocks (Fig. 15B).

Results

Fraser River Discharge

We selected discharge anomalies above and below the 5% level as years of above- and below-average discharge, respectively (Fig. 3B). The years in between were considered to be years of average discharge. Years of change to very high and very low discharge were identified using both the 2- and 3-yr anomalies described earlier. Both procedures identified anomalies, but because of the particular pattern of discharge, the 2-yr anomaly index appears to identify years of change slightly better than the 3-yr index that identified a slightly higher number of anomalous years. For

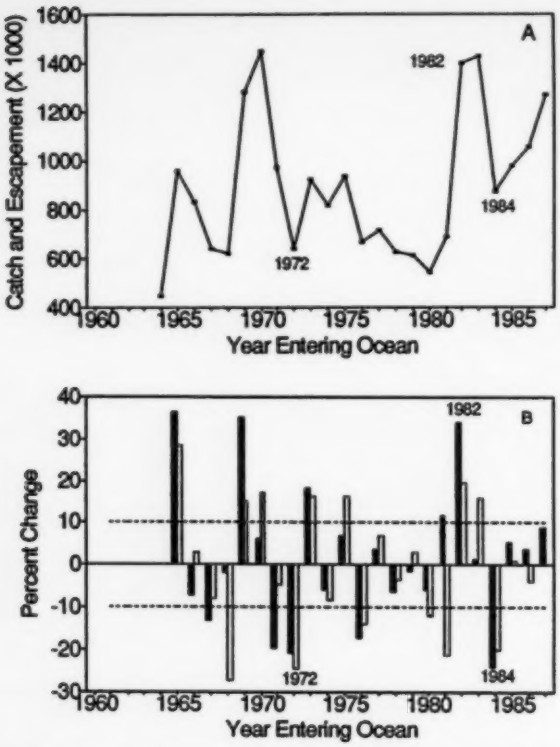


FIG. 12. (A) Catch and escapement of chum salmon produced in the Fraser River. The numbers are related to the year that the smolts entered the ocean. The catch year would be 2 yr later and the brood year would be 1 yr earlier. (B) The data in Fig. 12A expressed as a percent change. Years of anomalous good production were greater than 10%; years of anomalous low production were less than 10% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

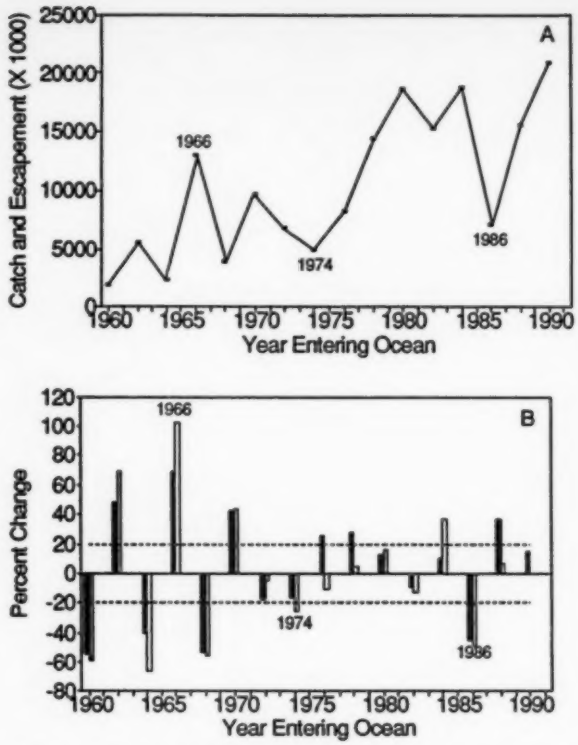


FIG. 13. (A) Catch and escapement of pink salmon produced in the Fraser River. The numbers are related to the year that the smolts entered the ocean. (B) The data in Fig. 13A expressed as a percent change. Years of anomalous good production were greater than 20%; years of anomnalous low production were less than 20% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

example, the 3-yr index identifies 1989 as a year of extremely low average discharge whereas this year is not anomalous in the 2-yr index. There is a change in discharge from 1986 to 1987 resulting in 1987 being identified as a low-discharge year and from 1989 to 1990 resulting in 1990 being a high-discharge year (Fig. 3), but 1989 is not a year of extreme change to either high or low discharge.

Despite some differences, both indices identified most of the same years as discharge anomalies. From 1960 to 1992, there were nine years identified as having extremely high discharge using the 2-yr index and 10 using the 3-yr index; seven years were the same for both indices. Similarly, there were 10 years identified as extremely low discharge using the 2-yr index and 12 using the 3-yr index; eight years were the same for both indices.

Chinook Salmon

We identified years of anomalously low and high production as values that exceeded 20% except for the sport catch where we used a 10% level. The 2-yr index of chinook age-2 abundance indicated that there were 18 of 30 years of anomalously high (9) or low (9) production (Fig. 5B). For the sport catch, 17 of the 30 years in the time series were identified as years of high (7) or low (10) production (Fig. 6B). Ten of 15 years were identified as having relatively high (4) or low (6) values in the hatchery survival data (Fig. 7B).

The 3-yr index of age-2 chinook abundance indicated that there were 22 of 30 years of anomalously high (10) or low (12) production (Fig. 5B). The 3-yr index of the sport catch indicated that 19 of 30 years were anomalously high (8) or low (11) (Fig. 6B) For hatchery survival, seven out of 15 years were anomalously high (3) or low (4) (Fig. 7B).

All of the chinook production anomaly indices were closely related to the pattern of Fraser River discharge (χ^2 test, $P < 0.05$ or 0.01) (Table 1). For all data series, anomalously high production of chinook salmon in the Strait of Georgia corresponded closely to the years of anomalously low Fraser River discharge, and anomalously low production of chinook corresponded closely to years of anomalously high Fraser River discharge. In the 2-yr index, only one of 25 anomalous years of low production occurred during an extreme change to low discharge and only two of 20 years of anomalously high production occurred during an extreme change to high discharge (Table 2). The 3-yr index comparisons were similar to the 2-yr index comparisons (Table 2). There were no years of very high production in years of

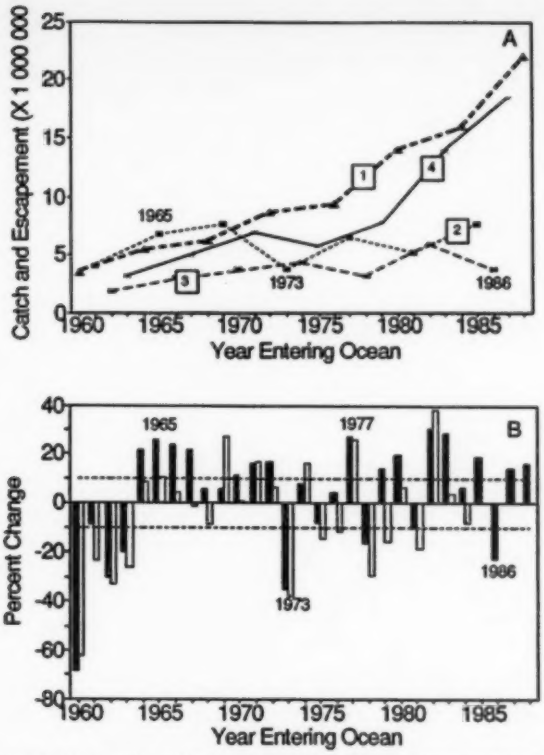


FIG. 14. (A) Catch and escapement of sockeye salmon produced in the Fraser River. The numbers are related to the year that the smolts entered the ocean. The catch year would be 2 yr later and the brood year would be 2 yr earlier. In general, there was not as much variation for sockeye as found for the catches of other salmon. There was a trend of rapidly increasing abundance beginning in the late-1970s in two of the lines. The 4-yr cycles are shown separately (labelled 1–4 consecutively). The strongest cycle is (1): the 4-yr cycle beginning in 1960. (B) The data in Fig. 14A expressed as a percent change. Years of anomalous good production were greater than 10%; years of anomalous low production were less than 10% (broken lines). The shaded bars represent the 2-yr changes and the empty bars the 3-yr changes.

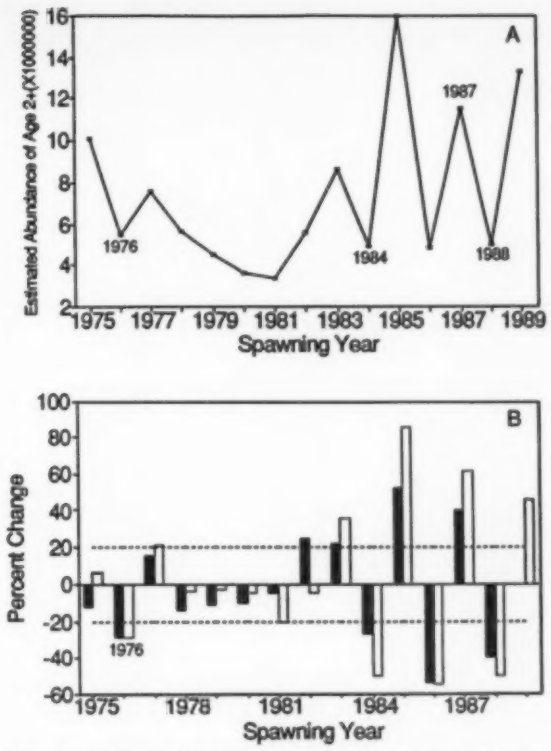


FIG. 15. (A) Estimated abundance of age-2+ herring in the Strait of Georgia. (B) The data in Fig. 15A expressed as a percent change. Years of anomalous good production were greater than 20%; years of anomalous low production were less than 20% (broken lines). The shaded bars represent the 2-yr changes and the open bars the 3-yr changes.

extreme increases in discharge, and only three of 27 years had very low production when discharge changed to a very low level (Table 2).

Coho Salmon

We identified years of anomalously high and low production as values that exceeded ±20% except for hatchery survival estimates where we used ±10% because the variations in the data were not as large as in the other series. Using the 2-yr index for the commercial catch anomalies, there were 17 of 31 years of either anomalously high (8) or low (9) commercial catches (Fig. 9B). In the 2-yr index of coho sport catch anomalies, 14 of 31 yr were anomalously high (7) or low (7) (Fig. 10B). In the 2-yr index of coho hatchery survival anomalies, seven out of 15 years were anomalously high (4) or low (3) (Fig. 11B).

The 3-yr index produced about the same number of anomalies in production. In the commercial catch, there were 21 of 31 years of either anomalously high (9) or low (12) catches (Fig. 9B). In the 3-yr index of coho sport catch, 12 of 31 years were high (6) or low (6) sport catches (Fig. 10B). In the 3-yr index of coho hatchery survival, nine out of 15 years were high (5) or low (4) (Fig. 11B).

All of the coho production anomaly indices were closely associated with the pattern of Fraser River discharge (χ^2 test, $P < 0.05$ or 0.01) except for the 2-yr index of hatchery survival (χ^2 test, $P < 0.25$) (Table 3). For the 2-yr indices, none of the 19 years of change to very low production occurred when discharge changed from very high to very low levels (Table 4). Only two of 19 years of above-average production occurred when discharge changed from very low to very high levels (Table 4). For the 3-yr indices, the results were very similar (Table 4). There were no years of very high production anomalies occurring in years with large increases in discharge and only two of 22 years of very low production when large declines in discharge occurred.

Chum Salmon

Percent differences greater than 10% were considered to represent years of anomalously high or low production. For the 2-yr index of extreme chum production, there were 11 of 23 years of anomalously high (6) and low (5) chum salmon production (Fig. 12B), and for the 3-yr indices, there were

TABLE 1. Relationship among the two Fraser River discharge anomaly indices and the 2- and 3-yr anomalies of chinook salmon production. Chi-square (χ^2) values are shown for each possible relationship and significance levels are indicated as $^{**}P < 0.05$, $^{***}P < 0.01$.

Fraser River discharge anomaly index	Age-2 abundance index		Sport catch		Hatchery survival	
	2-yr	3-yr	2-yr	3-yr	2-yr	3-yr
2-yr	10.00***		6.83**		7.88**	
3-yr		12.35***		9.28***		7.1**

TABLE 2. Numbers of extreme production anomalies of chinook salmon in relation to Fraser River discharge anomalies.

	Fraser River discharge anomaly					
	2-yr			3-yr		
Production anomaly	Very low	Average	Very high	Very low	Average	Very high
Very high	14	4	2	18	3	0
Very low	1	16	8	3	12	12

13 of 22 years of anomalously high (7) and low (6) chum salmon production (Fig. 12B). High chum salmon production anomalies rarely occurred in years of anomalously high discharge, and low chum salmon production anomalies rarely occurred in years of anomalously low discharge (Table 5). However, for neither the 2- nor the 3-yr chum salmon production indices was the relationship with discharge and anomalous production as close as was observed for chinook and coho salmon. A comparison of the 2-yr indices did indicate a weak relationship (χ^2 test, $P < 0.10$), but the comparison of the 3-yr indices did not reject the hypothesis that there was no relationship between anomalous production and discharge (χ^2 test, $P < 0.25$) (Table 6).

Pink Salmon

Anomalies greater than ±20% were chosen to represent years of anomalously high or low production. We were unable to reject the null hypothesis that there was no relationship between anomalous production of pink salmon and anomalous Fraser River discharge (Table 7). For the 2-yr index, 10 of 16 years had anomalously high (6) or low (4) pink salmon production (Fig. 13B). Using the 3-yr index, there were again 10 of 16 years of high (5) or low (5) production relative to the previous pink salmon production year (Fig. 13B). However, the hypothesis of no relationship between discharge and production anomalies was supported (χ^2 test, $P > 0.25$) (Table 7).

Sockeye Salmon

Anomalies greater than ±10% were chosen to be extreme for sockeye salmon. Production anomalies identified for each of the lines in a 4-yr cycle were combined into one data series to be compared with the discharge anomalies. Using the 2-yr index, there were 22 of 29 years of high (15) or low (7) sockeye production (Fig. 14B). Using the 3-yr index, there were 16 of 25 years of high (6) or low (10) sockeye production (Fig. 14B). There was no indication of a close relationship between discharge and production for either the 2- or 3-yr indices (Table 8).

Pacific Herring

Anomalies greater than ±20% were chosen to be extreme for Pacific herring. According to our 2-yr index, there were eight of 14 years of high (4) or low (4) Pacific herring production (Fig. 15B). In the 3-yr index, there were nine out of 14 yr of high (4) or low (5) herring production (Fig. 15B). The analysis of anomalous production of Pacific herring did not, in general, support the hypothesis of a close relationship between extreme anomalies in discharge and production (Table 9).

Discussion

Our study showed that the extreme Fraser River discharge anomalies are closely related to extreme year-to-year anomalies in the abundance and survival indices of chinook and coho salmon and probably less closely associated with chum salmon. In all of the observations for chinook and coho salmon, using all of the data series, large increases in catch or survival relative to the previous year rarely occurred for brood years that went to sea when there was a large increase in Fraser River discharge levels relative to the previous year. Similarly, large decreases in catch or survival relative to the previous year almost never occurred for brood years that went to sea in years when there was a large decrease in Fraser River discharge levels relative to the previous year. There was no indication of a close relationship between discharge anomalies and pink and sockeye salmon and Pacific herring production anomalies. The fact that it was possible to demonstrate a close relationship between discharge and chinook and coho production, despite the potentially confounding effects of fishing effort, escapement levels, freshwater habitat conditions, and potential data errors, clearly demonstrates that the pattern of Fraser River discharge affects the early marine survival of chinook and coho in the Strait of Georgia.

The method of identifying extreme anomalies had little effect on the acceptance or rejection of the null hypothesis for the chinook and coho abundance indices except that in some cases the level of significance was higher. The method used to select an anomaly did affect the acceptance of the relationship between extreme survival of coho reared in hatcheries and anomalous discharge. The 3-yr survival index and the 3-yr Fraser River discharge index were closely related (χ^2 test, $P < 0.05$) for coho hatchery survival anomalies, whereas a comparison using 2-yr indices was not

TABLE 3. Relationship among the two Fraser River discharge anomaly indices and the 2- and 3-yr anomalies of coho salmon production. Chi-square (χ^2) values are shown for each possible relationship and significance levels are indicated as $^{**}P < 0.05$, $^{***}P < 0.01$.

Fraser River discharge anomaly index	Commercial catch		Sport catch		Hatchery survival	
	2-yr	3-yr	2-yr	3-yr	2-yr	3-yr
2-yr	6.64***		7.8**		4.2	
3-yr		11.17***		9.0**		8.81**

TABLE 4. Numbers of extreme production anomalies of coho salmon in relation to Fraser River discharge anomalies.

	Fraser River discharge anomaly					
	2-yr			3-yr		
Production anomaly	Very low	Average	Very high	Very low	Average	Very high
Very high	12	5	2	18	2	0
Very low	0	8	11	2	9	11

TABLE 5. Numbers of extreme production anomalies of chum salmon in relation to Fraser River discharge anomalies.

	Fraser River discharge anomaly					
	2-yr			3-yr		
Production anomaly	Very low	Average	Very high	Very low	Average	Very high
Very high	4	1	1	5	1	1
Very low	0	2	3	1	2	3

related (χ^2 test, $P < 0.25$). In the case of hatchery survival data, we think that there may be a close relationship between extreme Fraser River discharge anomalies and changes in the annual survival of hatchery-reared coho but that the relationship does not appear to be as clear for hatchery survival as for the other indices. Hatchery-reared coho represent approximately 54% of the coho catch in the Strait of Georgia, 35% from Canadian hatcheries (Cross et al. 1991), and 19% from American hatcheries (R.J. Beamish and C.M. Neville, unpublished data). If catch anomalies are closely related to discharge anomalies and with hatchery-reared fish representing a large fraction of the catch, we would expect a close relationship between survival anomalies and discharge anomalies.

The selection of the anomaly index was also important for chum salmon. Only the 2-yr index of brood-year strength was weakly associated with discharge (χ^2 test, $P < 0.10$), but there was evidence of a production and discharge relationship. We interpret this to indicate that extreme discharge anomalies have an effect on chum salmon production, but the effects were not as clear or not as strong as was observed for chinook and coho from the data we used. The possibility of a relationship between chum salmon production anomalies and extreme discharge anomalies indicates that chum may reside in the Strait of Georgia longer than the 3–4 mo that was previously thought (Healey 1980).

Mechanism

A discussion of a possible mechanism is essentially an exercise in speculation; thus, we will keep our speculations brief. Assuming that most marine mortality occurs shortly after the salmon smolts enter salt water (Parker 1968; Bax 1983), fluctuating discharge could affect survival indirectly via the estuarine circulation or directly by physically affecting smolt distribution. We cannot prove that salmon smolts are not transported into areas less favourable for survival, but we favour a mechanism related to the estuarine circulation because our surveys in June and July 1990–1993 in the large plume of the Fraser River have not identified a movement of smolts out of the plume during high-discharge years (R.J. Beamish and C.M. Neville, unpublished data).

Nutrients in the bottom water in the Strait of Georgia are entrained into the surface waters as a consequence of the amount of turbulence at the interface between the bottom and surface layers (Farmer and Freeland 1983). It is the frequency of destabilization of the water column that appears to determine the level of nutrients in the surface or mixed layer. In the Strait of Georgia, there is less wind mixing of nitrate-rich deep water into the surface layer or euphotic zone during periods of high Fraser River discharge (St. John et al. 1992). Oceanographic factors other than discharge can also affect productivity (Harrison et al. 1983). Wind, light, and tides can be important but probably are less important, in general, than the amount of stability at the interface between the bottom and surface layers. In other words, there is a hierarchy of effects, as proposed by Levasseur et al. (1984) for the St. Lawrence River estuary. In periods of low discharge or decreased buoyancy of the surface layer, wind mixing would result in enhanced production. In fact, St. John et al. (1992) and Yin et al. (1995) observed that during periods of weak stratification, there was enhanced primary production after major wind events. In years of low or average discharge, wind, tides, and light should be important factors affecting the productivity of the surface layer. Our hypothesis is that the change to high discharge results in reduced availability of food for salmon which in turn increases the risk of predation as young salmon search for food. The opposite would occur during a change to low discharge.

Management Implications

This study and others (Drinkwater 1988) show that large sources of freshwater discharge can affect the survival of organisms in salt water. Fluctuations in total annual discharge are a common feature of the pattern of flow of the Fraser River. Records of this pattern go back to 1912 and

TABLE 6. Relationship among the two Fraser River discharge anomaly indices and the 2- and 3-yr anomalies of chum salmon abundance. Chi-square (χ^2) values are shown for each relationship and significance levels are indicated as $*P < 0.10$.

Fraser River discharge anomaly index	Fraser River production	
	2-yr	3-yr
2-yr	5.21*	
3-yr		4.11

TABLE 7. Relationship among the two Fraser River discharge anomaly indices and the 2- and 3-yr anomalies of pink salmon abundance. Chi-square (χ^2) values are shown for each relationship. None of the values were significant ($P < 0.10$).

Fraser River discharge anomaly index	Fraser River production	
	2-yr	3-yr
2-yr	1.48	
3-yr		1.2

TABLE 8. Relationship among the two Fraser River discharge anomaly indices and the 2- and 3-yr anomalies of sockeye salmon abundance. Chi-square (χ^2) values are shown for each relationship. None of the values were significant ($P < 0.10$).

Fraser River discharge anomaly index	Fraser River production	
	2-yr	3-yr
2-yr	1.28	
3-yr		1.07

TABLE 9. Relationship among the two Fraser River discharge anomaly indices and the 2- and 3-yr anomalies of Pacific herring abundance. Chi-square (χ^2) values are shown for each relationship. None of the values were significant ($P < 0.10$).

Fraser River discharge anomaly index	Strait of Georgia production	
	2-yr	3-yr
2-yr	3.0	
3-yr		3.21

presumably were common before discharge records were kept. If the interannual fluctuations have been common for centuries, it is possible that some species in the Strait of Georgia have adapted to this pattern of flow. Since 1976 there has been a declining trend in Fraser River discharge. If natural changes in discharge are occurring, it is important to recognize their impacts on marine survival and separate these effects from fishing and freshwater habitat effects when attempting to manage chinook and coho stocks.

The relationships between discharge and production anomalies may be useful in forecasting abundance changes. It is helpful to know if total coho catch in the Strait of Georgia could be higher or lower in the following year and chinook catch in 2 yr's time. However, the relationships apply only when extreme changes in discharge occur, and not when discharge is average or when consecutive years of above-average or below-average discharge occur. In 1990 and 1991, there were the first 2 consecutive yr of high discharge since 1922. In 1991, coho catches in the strait were extremely low (Fig. 8) and survival in general appears to have been low. The change to very low discharge in 1992 appears to be associated with very high catches of coho in the Strait of Georgia in 1993. However, 1993 was also a year of very low discharge, the lowest since 1945. The consecutive years of very low discharge in 1992 and 1993 were also the first since 1945 and it will be interesting to see how the catches of coho and chinook are in the Strait of Georgia in 1994 and 1995, respectively.

The value of the relationships in this report for fisheries management will improve as we understand more about the mechanisms involved. The pattern and possibly the amount of discharge are important but the physical and chemical composition of the bottom water that enters the Strait of Georgia as a consequence of the estuarine circulation probably is important also. We think that fisheries management will benefit from a better understanding of the relationships among Fraser River discharge and the marine environment.

References

ARGUE, A.W., R. HILBORN, R.M. PETERMAN, M.J. STANLEY, AND C.J. WALTERS. 1983. Strait of Georgia chinook and coho fishery. Can. Bull. Fish. Aquat. Sci. 211: 91 p.

BAX, N.J. 1983. Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) through Hood Canal - its variability and consequences. Ph.D. thesis, University of Washington, Seattle, Wash. 196 p.

BEACHAM, T.D., AND C.B. MURRAY. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. 44: 244–261.

BEACHAM, T.D., AND P. STARR. 1982. Population biology of chum salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia. Fish. Bull. (U.S.) 80: 813–825.

BEAMISH, R.J. 1993. Climate change and exceptional fish production off the west coast of North America. Can. J. Fish. Aquat. Sci. 50: 2270–2291.

COLLICUTT, L.D., AND T.F. SHARDLOW. 1992. Strait of Georgia sport fishery creel survey statistics for salmon and groundfish, 1991. Can. MS Rep. Fish. Aquat. Sci. 2137: 76 p.

CROSS, C.L., L. LAPI, AND E.A. PERRY. 1991. Production of chinook and coho salmon from British Columbia hatcheries, 1971 through 1989. Can. Tech. Rep. Fish. Aquat. Sci. 1816: 48 p.

DRINKWATER, K.F. 1988. The effect of freshwater discharge on the marine environment, p. 425–430. *In* W. Nicholaichuk and F. Quinn [ed.] Proceedings of a Symposium on the Interbasin Transfer of Water: Impact and Research Needs for Canada. Department of the Environment, National Hydrology Research Centre, Saskatoon, Sask.

ENVIRONMENT CANADA. 1990. Historical streamflow summary. British Columbia, Inland Waters Directorate. Waters Resources Branch, Water Survey of Canada, Ottawa, Ont. 351 p.

FARMER, D.M., AND H.J. FREELAND. 1983. The physical oceanography of fjords. Prog. Oceanogr. 12: 147–220.

FRASER, F.J., E.A. PERRY, AND D.T. LIGHTLY. 1983. Big Qualicum River salmon development project, Volume I: a biological assessment, 1959–1972. Can. Tech. Rep. Fish. Aquat. Sci. 1189: 198 p.

GROOT, C., AND K. COOKE. 1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related?, p. 53–60. *In* H.D. Smith, L. Margolis, and C.C. Wood [ed.] Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. Can. Spec. Publ. Fish. Aquat. Sci. 96.

HARRISON, P.J., J.D. FULTON, F.J.R. TAYLOR, AND T.R. PARSONS. 1983. Review of the biological oceanography of the Strait of Georgia: pelagic environment. Can. J. Fish. Aquat. Sci. 40: 1064–1094.

HEALEY, M.C. 1980. The ecology of juvenile salmon in the Georgia Strait, British Columbia, p. 203–209. *In* W.J. McNeil and D.C. Himsworth [ed.] Salmonid ecosystems of the North Pacific. Oregon State University Press, Corvallis, Oreg.

HEALEY, M.C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*), p. 311-393. *In* C. Groot and L. Margolis [ed.] Pacific salmon life histories. University of British Columbia Press, Vancouver, B.C.

HOLMES, M.A., AND D.W.A. WHITFIELD. 1991. User's manual for the commercial salmon catch spreadsheet program. Can. Tech. Rep. Fish. Aquat. Sci. 1807: 44 p.

HOURSTON, A.S., AND C.W. HAEGELE. 1980. Herring on Canada's Pacific coast. Can. Spec. Publ. Fish. Aquat. Sci. 48: 23 p.

INTERNATIONAL PACIFIC SALMON FISHERIES COMMISSION (IPSFC). 1965–85. Annual reports. IPSFC, Vancouver, B.C.

KUHN, B.R., L.L. LAPI, AND J.M. HAMER. 1988. An introduction to the Canadian database on marked Pacific salmonids. Can. Tech. Rep. Fish. Aquat. Sci. 1649: 56 p.

LEVASSEUR, M., J.-C. THERRIAULT, AND L. LEGENDRE. 1984. Hierarchical control of phytoplankton succession by physical factors. Mar. Ecol. Prog. Ser. 19: 211–222.

MOORE, R.D. 1991. Hydrology and water supply in the Fraser River Basin, p. 21–40. *In* A.H.J. Dorcey and J.R. Griggs [ed.] Water in sustainable development: exploring our common future in the Fraser River basin. Westwater Research Centre, University of British Columbia, Vancouver, B.C.

NEAVE, F. 1966. Pink salmon in British Columbia. Int. North Pac. Fish. Comm. Bull. 18: 71–79.

PACIFIC SALMON COMMISSION (PSC). 1986–89. Reports of the Fraser River panels on the Fraser River sockeye salmon fishing season. PSC, Vancouver, B.C.

PACIFIC SALMON COMMISSION (PSC). 1990. Report of the Fraser River panel to the Pacific Salmon Commission on the 1989 Fraser River sockeye and pink salmon fishing season. PSC, Vancouver, B.C.

PARKER, R.R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25: 757–794.

PRESS, W.H., B.P. FLANNERY, S.A. TEUKOLSKY, AND W.T. VETTERLING. 1986. Numerical recipes: the art of scientific computing. Cambridge University Press, Cambridge. 818 p.

PRITCHARD, D.W. 1967. What is an estuary: physical viewpoint, p. 52–63. *In* G.H. Lauff [ed.] Estuaries. American Association for the Advancement of Science, Washington, D.C.

SANDERCOCK, F.K. 1991. Life history of coho salmon, p. 395–445. *In* C. Groot and L. Margolis [ed.] Pacific salmon life histories. University of British Columbia Press, Vancouver, B.C.

SCHWEIGERT, J.F., V. HAIST, AND C. FORT. 1993. Stock assessment for British Columbia herring in 1992 and forecasts of the potential catch in 1993. Can. Tech. Rep. Fish. Aquat. Sci. 1913: 111 p.

ST. JOHN, M.A., S.J. MACDONALD, P.J. HARRISON, R.J. BEAMISH, AND E. CHOROMANSKI. 1992. The Fraser River plume: some preliminary observations on the distribution of juvenile salmon, herring and their prey. Fish. Oceanogr. 1: 153–162.

STOCKER, M., V. HAIST, AND D. FOURNIER. 1985. Environmental variation and recruitment of Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 42: 174–180.

THOMSON, R.E. 1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56: 291 p.

VERNON, E.H. 1982. Fraser River sockeye: the stocks and their enhancement. Mimeo. Rep., Department of Fisheries and Oceans, Pacific Region, Vancouver, B.C. 53 p.

WALDICHUK, M. 1957. Physical oceanography of the Strait of Georgia, British Columbia. J. Fish. Res. Board Can. 14: 321–486.

YIN, K., P.J. HARRISON, S. POND, AND R.J. BEAMISH. 1995. Entrainment of nitrate in the Fraser River estuary and its biological implications. II. Effects of spring vs neap tides and river discharge. Estuarine Coastal Shelf Sci. (In press)

Dietary Variation in a Freshwater Fish Species: Relative Contributions of Biotic Interactions, Abiotic Factors, and Spatial Structure[1]

Pierre Magnan and Marco A. Rodríguez[2]

Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, QC G9A 5H7, Canada

Pierre Legendre

Département de sciences biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, QC H3C 3J7, Canada

and Sylvain Lacasse

Département de chimie-biologie, Université du Québec à Trois-Rivières, C.P. 500, Trois-Rivières, QC G9A 5H7, Canada

Magnan, P., M.A. Rodríguez, P. Legendre, and S. Lacasse. 1994. Dietary variation in a freshwater fish species: relative contribution of biotic interactions, abiotic factors, and spatial structure. Can. J. Fish. Aquat. Sci. 51: 2856–2865.

We used multivariate analyses to examine which variables among the environmental and spatial components can best account for dietary variation in a freshwater fish, brook trout, *Salvelinus fontinalis*. The diet composition of brook trout was quantified in 37 lakes of the Laurentian Shield, Québec, Canada. Among the 25 measured environmental variables, fish species composition, sampling date, macrophyte abundance, and trout body length were the best predictors of diet composition. The total variation in diet composition was partitioned into four components: pure environmental 21.6%, pure spatial 23.2%, shared 19.9%, and unexplained 35.3%. A significant spatial trend in diet composition existed even after accounting for the main effects measured by the environmental variables. The two sets of spatial variables, when combined with the environmental descriptors, extracted different components of the dietary variation. The study allowed us to (1) highlight the role of spatial structure in diet variation of brook trout, (2) determine the relative contribution of both environmental and spatial components, and (3) generate testable hypotheses concerning mechanisms underlying the observed structure. Dependent variables other than diet composition, such as the density of different species at different sampling sites, can be used within the same statistical framework in studies of community ecology.

Nous avons utilisé des analyses multivariées pour déterminer quelles variables, parmi les composantes spatiale et environnementale, peuvent le mieux rendre compte de la variation dans l'alimentation d'une espèce de poissons d'eau douce, l'omble de fontaine, *Salvelinus fontinalis*. L'alimentation de l'omble de fontaine a été quantifiée dans 37 lacs du bouclier laurentien, Québec, Canada. Parmi les 25 variables environnementales mesurées, la composition en espèces de poissons, la date d'échantillonnage, l'abondance des macrophytes et la longueur des ombles ont été les meilleurs prédicteurs de l'alimentation. La variation totale de l'alimentation se distribuait à l'intérieur de quatre composantes : environnementale pure 21,6 %, spatiale pure 23.2 %, partagée 19,9 % et inexpliquée 35,3 %. Une tendance spatiale significative dans l'alimentation était toujours présente même après avoir tenu compte des effets principaux mesurés par les variables environnementales. Les deux ensembles de variables spatiales, lorsque combinés avec les descripteurs environnementaux, extrayaient différentes composantes de la variation de l'alimentation. Cette étude nous a permis de 1) mettre en lumière le rôle de la structure spatiale dans la variation de l'alimentation de l'omble de fontaine, 2) déterminer la contribution relative des composantes spatiale et environnementale et 3) générer des hypothèses testables concernant les mécanismes qui sous-tendent les structures observées. La composition de l'alimentation d'une espèce de poissons, l'omble de fontaine, a été utilisée comme variable dépendante dans nos analyses. Cependant, d'autres variables dépendantes, comme la densité de différentes espèces à différents sites d'échantillonnage, peuvent être utilisées à l'aide du même cadre statistique dans l'étude de l'écologie des communautés.

Received January 26, 1994
Accepted June 15, 1994
(J12252)

Reçu le 26 janvier 1994
Accepté le 5 juin 1994

[1]Contribution of the Groupe de recherche interuniversitaire en limnologie (GRIL).

[2]Present address: Département de biologie et des sciences de la santé, Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

Ecology is concerned not only with describing the patterns of distribution and abundance of species within communities, but also with determining the factors which are responsible for these patterns. It is now well recognized that biotic and abiotic factors may act jointly in structuring populations and communities (Schoener 1982; Danielson

1991; Dunson and Travis 1991; Norton 1991; Hart 1992). Although this pluralistic view is now well accepted, populations and communities are still often studied in a single-factor perspective, assuming that only one kind of factor (biotic or abiotic) plays a major role in structuring communities; these studies often focus on the effect of only one type of process (e.g., competition), presuming all other biotic and abiotic processes to have a neutral effect (Dunson and Travis 1991). Such an approach is not only biased, it also yields no information on the relative contributions of the biotic and abiotic factors or their interactions. When such interactions are not considered, one may overemphasize or misinterpret the effects of one or more factors, especially when these factors are intercorrelated (collinearity). Beyond the recognition that biotic and abiotic factors are jointly important in structuring communities, we need to evaluate which ones, among the biotic and abiotic variables, can best account for a given ecological structure such as the species abundances, or the pattern of resource use by species within communities. This is crucial not only to assess what are the most important variables, but also to determine which ones must be emphasized to better understand mechanisms underlying community organization (Schoener 1986; Persson and Diehl 1990).

It is also recognized that ecological patterns vary spatially. Regardless of habitat, components of population and community structure often exhibit consistent trends over environmental gradients (Menge and Olson 1990). Considering that biotic and abiotic factors vary spatially, another important issue in ecology is to determine the role of the spatial components in structuring populations and communities. Although ecologists have recently called for the inclusion of spatial structures in population and community investigations (see Ricklefs 1987; Legendre and Troussellier 1988; Bennett 1990; Menge and Olson 1990; Borcard et al. 1992; Levin 1992; Legendre 1993; Borcard and Legendre 1994), very few concrete approaches have been proposed. Furthermore, there is very little published work suggesting quantitative procedures for analyzing simultaneously the environmental (biotic and abiotic) and spatial components and determining their relative contributions in structuring a given ecological attribute such as the abundance or resource use of a species (e.g., Legendre and Troussellier 1988; Borcard et al. 1992).

The main objectives of this study are to determine (1) which variables, among the environmental and spatial components, can best account for diet variations in a freshwater fish species, the brook trout, *Salvelinus fontinalis*, and (2) what is the relative contribution (and statistical significance) of each of these components to the explained variance. A secondary objective is to suggest a statistical procedure, based on a combination of existing methods, which may be used to analyze the environmental and spatial components in population and community ecology. This procedure will also allow for the inclusion of a temporal component, which may be as important as the environmental and spatial components to explain variations in seasonally fluctuating environments (e.g., Bennett 1990).

Biological Background

The brook trout is found in sympatry with the northern redbelly dace, *Phoxinus eos*, the creek chub, *Semotilus atromaculatus*, and the white sucker, *Catostomus commersoni*, in many oligotrophic lakes of southern Québec, Canada. Cyprinids and catostomids were introduced in these lakes by bait fishermen 30–70 yr ago, or colonized these habitats after natural barriers disappeared following the use of splash dams for log transport, a practice commonly used at the beginning of the century (Bilby and Ward 1991; Lacasse and Magnan 1994). Brook trout colonized the area following the last glaciation (Lacasse and Magnan 1994). A survey done by the Québec Government in the 1970's revealed that among the 329 lakes found in our study area (Mastigouche and Saint-Maurice reserves; 45°73′N, 73°17′W), 41% contained allopatric brook trout populations (i.e., with no other fish species present), 33% contained trout and northern redbelly dace, 26% contained trout and creek chub, 20% contained trout and white sucker, and 20% contained more than two introduced species with brook trout (note that percentages do not add to 100 because there is overlap in category membership). These are typical small oligotrophic lakes with respect to surface area, mean depth, conductivity, Secchi disk transparency, thermal stratification, and oxygen concentration (Magnan 1988, 1989). All lakes in the present study are located within a 3000-km^2 area.

The impact of introduced species on brook trout populations has been investigated since 1978 in this study area, mainly by comparing allopatric brook trout with populations living sympatrically with introduced species. There is no lake in the area containing only dace, chub, or sucker. In this kind of study, comparisons are often done based on only one unit of each type of community. A major criticism of this approach is that comparisons that use single sampling units (here, lakes) may not always be valid because observed differences may be due to factors other than the presence or absence of a given species (Sale 1979; Diamond 1986). In order to minimize this potential source of error, some authors have made comparisons on replicates of allopatric and sympatric brook trout populations (Magnan and FitzGerald 1982; Magnan 1988; Lachance and Magnan 1990a, 1990b; East and Magnan 1991; Magnan and Stevens 1993; Rodríguez and Magnan 1993). Another approach has been to study different kinds of dependent variables (e.g., components of brook trout diet, density, biomass, and mean length of planktonic prey in the resource) using multiple linear regression models (Lacasse and Magnan 1992; Rodríguez et al. 1993). More detailed studies investigating spatial distributions of the fish, as well as their feeding habits in terms of prey type, prey size, and seasonal variation, have been done on subsets of the lakes (Magnan and FitzGerald 1982, 1984a; Naud and Magnan 1988; Tremblay and Magnan 1991). Finally, studies investigating foraging and aggressive behavior of the fish have been conducted in the laboratory, in order to explain specific results obtained in the field (Magnan and FitzGerald 1984b; East and Magnan 1991).

The presence of creek chub and white sucker significantly reduces the sportfishing yield (kilograms per hectare per year) of brook trout (Magnan 1988). Gillnet fishing and field experiments have revealed that the relative abundance of brook trout, in terms of catch per unit of effort, is significantly lower in lakes containing white sucker in which most of the mortality occurs in the period between hatching (in April) and the beginning of June (Lachance and Magnan 1990a; Venne and Magnan 1995). One of the most striking

effects of competing species involves the feeding habits of brook trout (Magnan and FitzGerald 1982; Magnan 1988; Lachance and Magnan 1990b; East and Magnan 1991; Tremblay and Magnan 1991; Lacasse and Magnan 1992). In allopatry, brook trout feed mostly on benthic invertebrates of the littoral zone, e.g., Diptera, Trichoptera, Megaloptera (Sialidae), Ephemeroptera, and Odonata. In contrast, trout living in sympatry with creek chub and white sucker shift their food habits to prey found in the pelagic zone (open water) such as zooplankton (mostly *Daphnia* and *Holopedium*), swimming and emerging aquatic insects, dipteran pupae, terrestrial insects, and, to some extent, prey fish (almost exclusively northern redbelly dace). This diet shift of sympatric brook trout is correlated with a shift in their spatial distribution within lakes (Magnan and FitzGerald 1982; Tremblay and Magnan 1991), with significant changes in gill rakers and pyloric caecal morphology (Magnan 1988; Magnan and Stevens 1993), and with significant changes in the structure of the zooplankton community (Magnan 1988; Rodríguez et al. 1993). Creek chub and white sucker, which feed mostly on benthic invertebrates, appear to be better adapted (morphologically and behaviorally) than brook trout to feeding on bottom prey (Magnan and FitzGerald 1984b; Magnan 1988; Tremblay and Magnan 1991).

Between May and July, the benthic resources tend to decrease in abundance (Magnan and FitzGerald 1982; Tremblay and Magnan 1991; Rodríguez and Magnan 1993). Competition between brook trout and introduced species for benthic resources is stronger when food is scarce; therefore, as summer advances, trout feed more intensively on the open-water prey and less on benthos. Another factor that should contribute to this seasonal shift of trout to the pelagic zone is the increase of water temperature in the littoral zone during the summer (Tremblay and Magnan 1991). This may have more of an influence on trout than on sucker because of their different thermal preferendum (16.1°C for brook trout versus 21.0°C for white sucker; Wismer and Christie 1987).

For all the response variables for which we have compared the effects of creek chub and white sucker (yield, feeding habits, length of the gill rakers of brook trout, zooplankton community structure), the impact of sucker tends to be stronger than that of chub. This could be explained by the fact that white sucker may use significant amounts of zooplankton, which is the main competitive "refuge" along the food axis for trout in these lakes. Small white sucker (1.3–2.3 cm) are planktivorous (Carlander 1969; Scott and Crossman 1973), and larger ones may feed heavily on cladocerans, especially late in the summer (Tremblay and Magnan 1991).

Multiple linear regression analyses have indicated that the presence of introduced species is not the only determinant of the diet of brook trout; for example, the independent variables, presence of chub and sucker, zooplankton community structure, sampling date, morphoedaphic index, and importance of rock outcrops, accounted for 88% of the variation in mass of zoobenthos eaten by trout, which was the preferred prey in allopatry (Lacasse and Magnan 1992). In another model, 30% of the variation in mass of zooplankton eaten by trout was explained by the importance of macrophytes and refuges for fish (trout or their prey). Models for the abundance of amphipods, dipteran pupae, swimming insects, terrestrial insects, and prey-fish in the diet explained between 36 and 63% of the variation; the presence of white sucker or an index of their impact (mean length or density of Cladocera) and at least two habitat characteristics (e.g., pH, transparency, slope, morphoedaphic index, rocks and rock outcrops, emergent vegetation, macrophyte importance, and refuge for fish) appeared in each of these models (Lacasse and Magnan 1992).

The Approach

Community data typically involve numerous sites and species, which naturally lead one to rely on multivariate analyses to summarize the data while minimizing distortion of the spatial arrangement of sites or species (Gauch 1982; Legendre and Legendre 1983; Pielou 1984; Jackson et al. 1992). Conventional clustering and ordination methods are powerful tools for pattern detection and for synthesizing multivariate ecological data, but these methods are limited in their ability to detect relationships between community attributes and predictor variables and to assess the statistical significance of putative relationships. This can lead to overinterpretation of patterns that are not biologically or statistically significant (Jackson et al. 1992).

In the following section, a flexible and general statistical framework is presented that can be used to estimate the effects of independent environmental and spatial variables on multivariate community attributes and to assess the statistical significance of these relationships. In the first step of our analysis, the trout diet composition, which we have quantified in different lakes, was related to three sets of predictor variables separately: environmental (biotic and abiotic), geographic coordinates, and drainage pattern; these last two sets represent different ways of looking at the spatial organization of our fish populations. Each set of variables (diet, environmental, and spatial) was represented as a "variable by lake" matrix. Then in a second step, to determine whether the interpretation of trout diets on the basis of environmental variables could be enhanced by inclusion of the spatial structure (geographic location or drainage pattern), the total variation in trout diet composition was partitioned into independent components representing the relative contributions of the different sets of predictor variables. Used in combination with permutation tests, this procedure allowed us to evaluate the magnitude and statistical significance of effects associated with each component.

Materials and Methods

We used the same environmental and diet data as Lacasse and Magnan (1992), while spatial variables were quantified specifically for this study. Detailed information on the study area, field methods, and laboratory procedures can be found in Lacasse and Magnan (1992). Therefore, only a brief summary is presented here.

Study Lakes

Data on trout diet were collected in 42 lakes in the Mastigouche Reserve, Québec (46°40′N, 73°20′W). Analyses relating diet composition to environmental variables were performed only on the 37 lakes for which complete sets of environmental data were available. The study lakes were assigned to three major types according to fish species composition (Magnan 1988; Lacasse and Magnan 1992). Among the

37 lakes, 12 contain brook trout ("trout" lakes), 12 contain brook trout and creek chub ("chub" lakes), and 13 contain brook trout and white sucker ("sucker" lakes). Creek chub and pearl dace (*Margariscus margarita*, formerly *Semotilus margarita*) are also present in some of the sucker or chub lakes, but their relative biomass is less than 1% in these lakes (Magnan 1988). Northern redbelly dace is found in most of the lakes but does not affect the mean yield of brook trout in the study area (Magnan 1988).

Trout Diet Composition

Stomachs (a mean of 20 per lake) were sampled from brook trout captured during daytime by anglers between 1 and 30 June 1989. The mean percent wet mass (Hyslop 1980) of each of nine functional prey categories, reflecting differences in microhabitat utilization, was recorded in the laboratory: zoobenthos (mostly Diptera, Ephemeroptera, Odonata, and Trichoptera larvae), amphipods (mostly Gammaridae), zooplankton (mostly Cladocera and Chaoboridae), dipteran pupae, aquatic insects (Hemiptera and Coleoptera), terrestrial insects, prey-fish (mainly northern redbelly dace), leeches, and "other" prey items.

Environmental Variables

Lake maximum depth, surface area, volume, and perimeter were obtained from 1:20 000 bathymetric maps. Epilimnetic temperature at 0.5 m, conductivity, pH, and Secchi disk transparency were measured in the field, as were the percentages of the shoreline containing submerged wood, herbs, shrubs, beach, mudflats, rocks, and rock outcrops. Macrophyte abundance was coded as an ordinal index from 0 to 5. Temperature profiles and bathymetric maps were used to estimate the area contained within the thermal optimum zone (13–17°C) for brook trout (Lacasse and Magnan 1992). A binary variable was used to code whether the littoral zone overlapped the thermal optimum. The numerical density, biomass, and mean length of cladocerans were estimated from triplicate samples collected in midlake. Mean fork length was used as a measure of brook trout size. Sampling date, within the month of June 1989, was included as an environmental covariable to account for seasonal trends over the sampling period. Fish species composition was coded using three binary dummy variables, TROUT, CHUB, and SUCKER, to label the three lake types "trout", "chub", and "sucker" as follows:

	Dummy variable		
Lake type	TROUT	CHUB	SUCKER
Trout	1	0	0
Chub	0	1	0
Sucker	0	0	1

Although in general, only two categorical variables are required to distinguish among three categories (Montgomery and Peck 1982), this particular coding is used by program CANOCO (ter Braak 1990a). This is more appropriate than coding trout = 1, chub = 2, and sucker = 3 because the latter coding arbitrarily imposes a potentially misleading ordering of treatment effects (Montgomery and Peck 1982).

Spatial Variables

The geographic coordinates for the lake, as well as the pattern of interconnections among lakes, were obtained from 1:50 000 and 1:250 000 government maps. The matrix of two-dimensional geographic coordinates was completed, following Legendre (1990), by including all terms for a cubic trend surface polynomial; this procedure allows one to estimate the parameters of a trend surface regression equation of the form

$$Z = b_1X + b_2Y + b_3XY + b_4X^2 + b_5Y^2 + b_6X^2Y + b_7XY^2 + b_8X^3 + b_9Y^3$$

where X is longitude and Y is latitude in Cartesian coordinates. This equation represents a geographic surface that can be used to describe how a summary measure of the trout diet (the Z variable, which in this study takes the form of ordination axis scores) varies over the matrix of X–Y coordinates. Inclusion of quadratic, cubic, and interaction terms in the equation allows us to model not only simple linear gradient patterns but also more complex features such as patches or gaps (Borcard et al. 1992). Geographic coordinates were centered to zero mean before computing the higher terms of the polynomial to reduce nonessential collinearity when fitting the polynomial (Montgomery and Peck 1982).

The pattern of lake interconnections was quantified following the method proposed by Kluge and Farris (1969) for coding a character transformation series in phylogenetic analysis. The procedure can be briefly summarized as follows. A hydrographic "tree" is built that maps the connections among lakes (Fig. 1). A node number is then assigned to each of the bifurcations or branching points in the tree. Each lake is characterized by the sequence of nodes along the direct path connecting the lake to the "root" or base of the tree. A lakes-by-nodes matrix is constructed by assigning, for each lake, a value of 1 to all nodes connecting it to the root and 0 to all other nodes. Two special cases deserve special attention. First, lakes forming a node (i.e., the lake receives inflows from more than one subbasin: nodes 5, 6, 17, and 26 in Fig. 1) were coded 0 for that node because it is not located downstream from that lake. Second, lakes positioned on branches between two bifurcations (e.g., the three lakes along the minor branch created by node 10 in Fig. 1, or the lakes between nodes 16 and 17) were not given special node numbers and were assigned the same node values because all these lakes belong to the same subbasin. The matrix resulting from this procedure contains a complete numerical coding of the drainage basin pattern depicted by the hydrographic tree.

Statistical Framework

Trout diet composition was related to the three sets of predictor variables separately (environmental, geographic coordinates, and drainage pattern) by canonical correspondence analysis (ter Braak 1986), an eigenvalue ordination technique especially designed for direct analysis of the relationships between multivariate ecological data tables. Ordination scores were used to create a scattergram that simultaneously represents the dietary items, the environmental variables (biotic and abiotic), and the study lakes. For each set of independent variables, the best predictors were selected using a forward selection procedure available in version 3.1 of program CANOCO (ter Braak 1988b; program available from C.J.F. ter Braak, Agricultural Mathematics Group, TNO Institute for Applied Computer Science, Box 100, NL-6700 AC Wageningen, The Netherlands), with a cutoff point of $p = 0.10$.

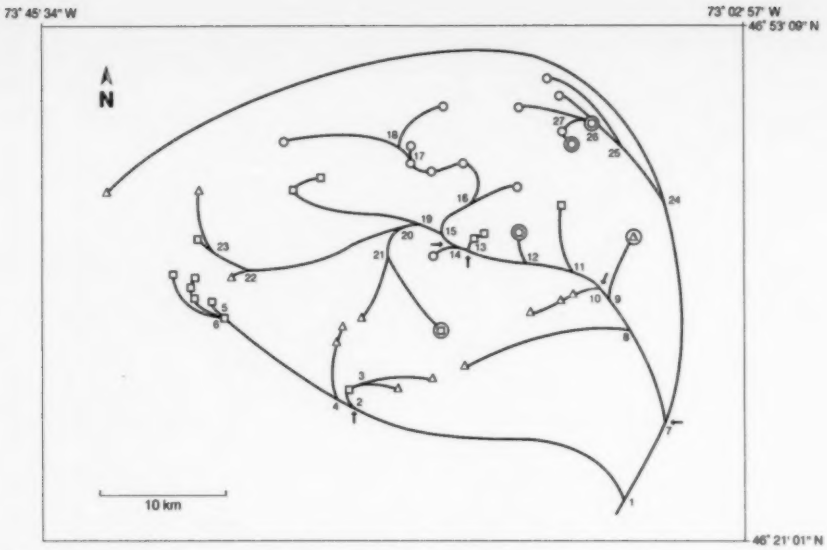


FIG. 1. Schematic representation of geographic locations and interconnections among the study lakes. Lakes enclosed by a circle were not included in canonical correspondence analyses (see Materials and Methods). Circles, trout lakes; triangles, chub lakes; squares, sucker lakes. Numbers (1–27) represent nodes of the hydrographic network (see Materials and Methods: Spatial Variables).

Multivariate tests for overall differences in diet composition among lake types were made with canonical correspondence analysis, using only as predictor variables the dummy variable coding for fish species composition, as described by ter Braak (1987).

Following the study of trout diet composition as a function of the three sets of predictor variables separately, trout diet variation was analyzed against the environmental and spatial variables together, using the method of variation partitioning proposed by Borcard et al. (1992) and Borcard and Legendre (1994). The purpose now is to determine whether interpretation of trout diets on the basis of environmental variables could be enhanced by inclusion of the spatial structure (geographic location or drainage pattern); following this analysis, the total variation in trout diet composition was partitioned into four independent components ("pure" environmental, "pure" spatial, spatial component of environmental variation, and unexplained) by canonical and partial canonical correspondence analysis (ter Braak 1986, 1988a). This procedure involves the following steps: (1) compute the variation accounted for by the environmental variables; (2) compute the variation accounted for by the spatial variables; (3) compute the variation explained by the environmental variables after removing by partial canonical correspondence analysis the effect of the spatial variables; (4) compute the variation explained by the spatial variables after removing the effect of the environmental variables by partial canonical correspondence analysis. The total explained variation (r^2) is the sum of the explained variations in (1) and (4) or in (2) and (3). The nonspatial ("pure") environmental variation is given by step (3), and the ("pure") spatial variation that is not related to the environmental variables is given by step (4). The spatially structured environmental variation, or variation "shared" by the spatial and environmental variables, is obtained by subtracting (3) from (1) or (2) from (4). The unexplained portion of variation is obtained by subtracting the "pure" environmental variation, the "pure" spatial variation, and the "shared" variation from the total variation. Variation partitioning was performed in two parallel sets of analyses, one including environmental variables and geographic coordinates and another including environmental variables and drainage pattern. Then, to determine whether the two sets of spatial variables extracted different (nonoverlapping) components of the dietary variation, an extension of this method, incorporating simultaneously the three sets of explanatory variables, was used to partition the total variation. The statistical significance of the environmental and spatial components was evaluated by Monte Carlo permutation tests of the sum of all eigenvalues, as implemented in CANOCO.

Results

Overall, the dietary items were found in the following relative abundances: zoobenthos (43.8%), zooplankton (23.6%), aquatic insects (7.2%), dipteran pupae (6.9%), terrestrial insects (6.2%), prey-fish (5.2%), others (2.6%), amphipods (2.6%), and leeches (1.9%).

Environmental Variables

Among the 25 environmental variables initially considered for inclusion in the canonical correspondence analyses, only five were retained by the forward selection procedure: macrophyte abundance, the dummy variable trout (which separated trout lakes from chub lakes and sucker lakes), sampling date (within the same month), pH, and mean fish length. None of the pairwise correlations among these five environmental variables exceeded 0.19. Combined, these five variables account for 41.6% of the total variation in trout diet composition. The first ordination axis extracted by canonical correspondence analysis accounts for 16.3% of the variation; it

TABLE 1. Summary statistics for canonical correspondence analysis of brook trout diet and environmental variables. Eigenvalues were 0.165 for axis 1 and 0.115 for axis 2. *$p < 0.05$.

	Canonical coefficients		Correlations with canonical axes	
	Axis 1	Axis 2	Axis 1	Axis 2
Date	0.26*	−0.03	0.48*	−0.16
Macrophytes	0.07	−0.29*	0.19	−0.62*
pH	0.04	−0.12	−0.04	−0.31
Fish length	−0.15*	−0.09	−0.31	−0.20
Trout lake	−0.26*	−0.08	−0.52*	−0.25

TABLE 2. Canonical coefficients for individual predictor terms in analyses with spatial variables as predictors. In the geographic coordinate analysis, eigenvalues were 0.111 for axis 1 and 0.066 for axis 2; in the drainage pattern analysis, eigenvalues were 0.210 for axis 1 and 0.110 for axis 2. *$p < 0.05$.

Geographic coordinates			Drainage pattern		
Predictor	Axis 1	Axis 2	Predictor	Axis 1	Axis 2
X	0.34*	0.17	Node 2	0.13	0.29*
Y	−0.30*	0.09	Node 10	0.67*	−0.01
X^2	0.22	−0.23	Node 13	−0.28	0.48*
Y^2	−0.17*	0.01	Node 14	−0.37*	−0.34*
X^3	0.03	−0.47*			

primarily reflects differences due to fish species composition, seasonal change, and fish length (Table 1). The second axis accounts for an additional 12.7% of the variation and reflects a gradient in pH and macrophyte abundance (Table 1). Diet composition and environmental variables are significantly related ($p = 0.001$), as shown by a Monte Carlo permutation test (1000 permutations) for the sum of all canonical eigenvalues (ter Braak 1990a).

Representation of lakes, dietary items, and environmental variables on an ordination diagram (Fig. 2) shows that 33 of the 37 lakes are grouped into an elongated cluster that runs from center-left to bottom-center of the graph, diagonal to axes 1 and 2. A cluster analysis (not presented here) performed on the coordinates for the first two ordination axes (UPGMA algorithm based on Euclidean distance, misleadingly called "average linkage" in the SYSTAT program; Wilkinson 1990) clearly separated the lakes in the elongated cluster from the four outlying lakes. These four lakes lie outside the cluster mainly because of the high percentage of prey-fish consumed by brook trout in these lakes, as indicated by the symbol for prey-fish in the ordination plot and by direct comparison with percent consumption (26–46%, in contrast with 0–12% for all other lakes). High consumption of prey-fish in these lakes is related to high macrophyte abundance and late collection of samples (Fig. 2). Approximate t-tests (ter Braak 1990b) yielded significant results ($p < 0.05$) for both relationships. None of the other environmental variables was related significantly to consumption of prey-fish. The graph also indicates that amphipods were consumed more often in lakes with high macrophyte abundance ($p < 0.05$).

The most salient contrast in diet composition among the 33 lakes in the elongated cluster (Fig. 2) is between lakes in which zoobenthos is the major diet item (upper left of cluster) and those in which zooplankton, overall the second most abundant diet item, is consumed together with alternative prey (lower right of cluster). This contrast is most strongly associated with the dummy variable trout lake, as indicated by the alignment of the main axis of the cluster and the arrow for trout and by the length of this arrow (Fig. 2). The presence of creek chub or white sucker seems to cause a marked shift from zoobenthos, the dominant food item in trout lakes, to alternative prey; also, this shift becomes more pronounced as summer progresses, from 1 to 30 June. This interpretation, based on the ordination plot, is confirmed by direct comparison of percent consumption: zoobenthos accounts for an average of 60.3% of stomach contents in

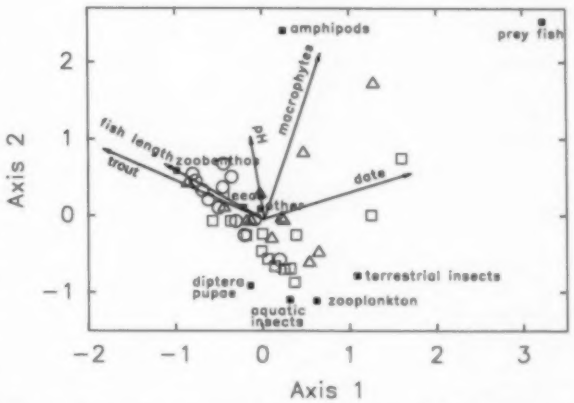


FIG. 2. Canonical correspondence ordination of lakes, diet items, and environmental variables. Open circles, trout lakes; open triangles, chub lakes; open squares, sucker lakes. Diet items are represented by solid squares. The environmental variable arrows are drawn from the centroid of the lake dispersion.

trout lakes (>50% in 11 of 15 lakes) whereas zoobenthos content averages 34.6% in chub and sucker lakes combined (>50% in 7 of 27 lakes).

Spatial Variables

The best model relating diet composition to geographic coordinates accounts for 30.4% of the total variation and includes five terms after forward selection:

$$Z = b_1X + b_2Y + b_3X^2 + b_4Y^2 + b_5X^3.$$

Axis 1 accounts for 13.2% of the variation and axis 2 accounts for an additional 7.0% of the variation. The main dietary items providing contrast among lakes along axis 1 (determined mostly by terms X, Y, and Y^2; Table 2) are zoobenthos, which has the largest negative score, and prey-fish and terrestrial insects, which have large positive scores (Table 3). For axis 2 (determined mostly by term X^3; Table 2), the strongest contrast is provided by zooplankton versus prey-fish (Table 3).

The best model relating diet composition to the drainage pattern accounts for 29.5% of the total variation and includes nodes 2, 10, 13, and 14 (Fig. 1) as predictor terms, after forward selection; node 2, which is redundant with node 7 because all lakes included in node 2 are excluded from

TABLE 3. Ordination scores for dietary items in canonical correspondence analyses with spatial variables as predictors.

	Geographic coordinates		Drainage pattern	
	Axis 1	Axis 2	Axis 1	Axis 2
Zoobenthos	−0.78	−0.71	−0.66	−0.64
Amphipods	0.12	0.83	0.62	−3.34
Zooplankton	0.21	1.53	−0.15	0.80
Dipteran pupae	−0.41	0.50	−0.09	1.65
Aquatic insects	0.48	0.60	0.32	1.20
Terrestrial insects	1.15	−0.16	1.34	0.54
Prey-fish	3.26	−1.66	3.42	−0.88
Leeches	−0.16	−0.98	−0.30	−1.53
Other	0.32	0.13	0.04	−0.16

node 7 and vice versa, was eliminated by the forward selection procedure. Axis 1 accounts for 17.7% of the variation and axis 2 accounts for an additional 8.0% of the variation. The main dietary items providing contrast among lakes along axis 1 are zoobenthos and leeches versus prey-fish and terrestrial insects (Table 3). For axis 2, the strongest contrast is provided by amphipods and leeches versus dipteran pupae and aquatic insects (Table 3).

Components of Variation

Partitioning of the variation (Fig. 3) indicates that the environmental and the spatial variables together account for 56.8% of the total variation when the geographic coordinates are used and for 50.7% of the variation when the drainage pattern is used. The "pure" spatial component contributes substantially to the total variation (15.3% for geographic coordinates, permutational probability for the sum of all eigenvalues $p = 0.011$ after 1000 permutations; 9.2% for drainage pattern, permutational $p = 0.001$ after 1000 permutations), but still a relatively large portion of the total variation (43–49%) is left unexplained. The component of variation shared by the environmental and spatial variables is higher for the drainage pattern (20.2%) than for the geographic coordinates (15.1%).

The "pure" spatial component (15.3%; $p = 0.011$) associated with the geographic coordinates can be visualized by drawing on a map a series of isopleths that connect points with the same value for axis 1 (Fig. 4), as recommended by Borcard and Legendre (1994). The picture clearly illustrates the significant spatial trend (decrease in axis 1 scores along a west–northeast gradient) that remains in the diet data even after accounting for the main effects measured by our environmental variables. When these environmental effects are held constant by partial canonical analysis (see Materials and Methods), inspection of axis 1 scores for dietary items (given in parentheses) reveals that there was a tendency for relative abundance of amphipods (2.6) and of zooplankton (1.3) in the diet to be largest in lakes with high axis 1 values (west on the map) whereas prey-fish (−1.4), terrestrial insects (−1.6), dipteran pupae (−1.3), and leeches (−2.0) tended to be most abundant in diets of trout from lakes with low axis 1 values (northeast). Zoobenthos (−0.17), aquatic insects (0.18), and others (0.41) have intermediate values for axis 1.

In a partial canonical correspondence analysis controlling for the effect of both the environmental and drainage pattern

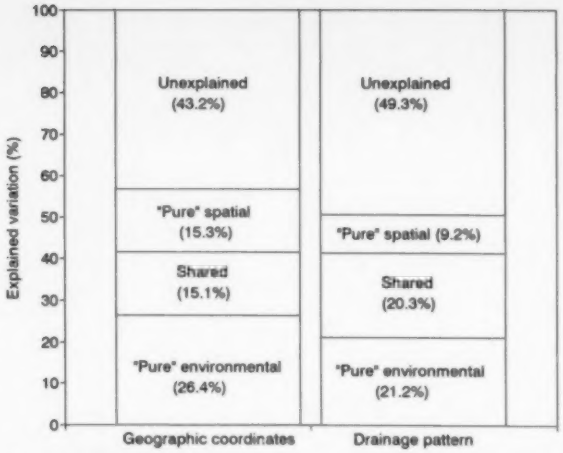


FIG. 3. Partition of the total variation in diet composition into four independent components: "pure" environmental, "pure" spatial, spatial component of environmental variation ("shared" variation), and unexplained. Left: Analysis with environmental variables and geographic coordinates as predictors. Right: Analysis with environmental variables and drainage pattern as predictors.

variables, the geographic coordinates still explained a significant part (28.4%; permutational probability for the sum of all eigenvalues $p = 0.013$ after 1000 permutations) of the remaining variation in diet composition; this part is equal to 14.0% of the total variation. This demonstrates that the two sets of spatial variables, when combined with the environmental descriptors, extract different, largely nonoverlapping components of the dietary variation. A partition of the total variation using the three sets of explanatory variables (Fig. 5) revealed that the environmental variables combined with both sets of spatial variables account for 64.7% of the total variation. The portion of variation corresponding uniquely to the environmental variables (21.6%) is larger than the portions corresponding uniquely to either the geographic coordinates (14.0%) or the drainage pattern (7.9%). Most of the explained variation is accounted for by these three portions (43.5% of the total variation) plus the portion that is simultaneously shared by the three sets of explanatory variables (15.4% of the total variation) (Fig. 5). The negative value −0.3% in Fig. 5 results from calculation of variation components by difference, and should be interpreted as being approximately zero.

Discussion

The present study allowed us to highlight the role of the spatial structure in the dietary variation of brook trout and to determine the relative contributions of the environmental and spatial components to the observed structure. Outside of, and in addition to, the classical environmental control of species (according to Table 1, the most important environmental variables are fish species composition, date of sampling, macrophyte abundance, and trout body length), this study demonstrates that other geographically structured factors are at work. There may be, of course, spatially structured environmental variables that were not taken into account in our study, and these may be determinants of trout diet; or, this spatial structure may reflect trout genetic factors that happen

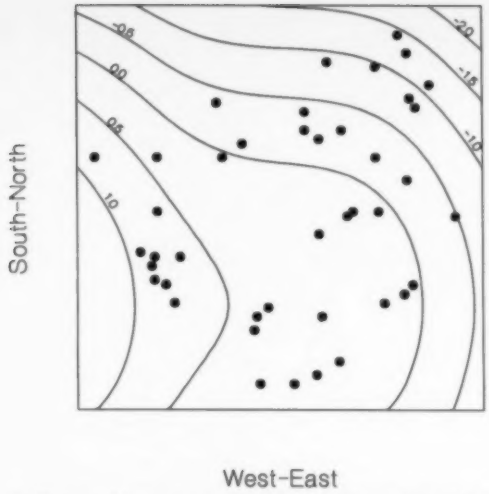


FIG. 4. Geographic map representing the "pure" spatial variation in diet composition (from the geographic coordinate analysis). Each point represents a lake. The curves are fitted isopleths for axis 1 values (see Results).

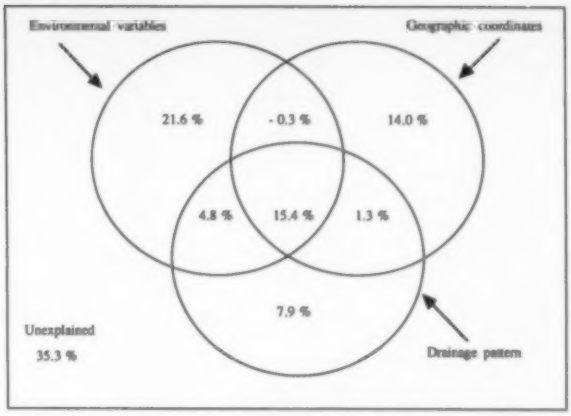


FIG. 5. Venn diagram showing the partition of the total variation in diet composition explained by the three sets of explanatory variables. The negative value −0.3% results from calculation of variation components by difference, and should be interpreted as being approximately zero.

to have a spatial structure because of historical events such as dispersal of species through the river drainage system or of introduction of bait species from roadways (details below). Before the present study, although the effect of the environmental component (biotic and abiotic factors) on brook trout diet had been documented in the system under study here, nothing was known concerning the spatial structure of this response variable or the interaction between the environmental and spatial components.

With regard to the role of the environmental variables, the results of the present analysis were consistent with studies previously undertaken in the same study system (see section describing the system). Moreover, because the present analysis simultaneously related all the components of fish diet with the environmental variables, which had not been done in these previous studies, it was possible to determine the relative contribution of the different independent biotic and abiotic variables (as indicated in the ordination analysis by the alignment of the main axis of the cluster and the arrows of the different variables, and by the length of these arrows). The presence of creek chub or white sucker caused a marked shift from zoobenthos, the dominant food item in allopatry, to zooplankton and other alternative prey; this shift became more pronounced as the summer progressed. Also, high consumption of prey-fish was related to high macrophyte abundance and late sampling date. Finally, the occurrence of amphipods in the diet was related to pH and to macrophyte abundance. Together, these environmental variables accounted for 41.6% of the total variation in trout diet composition.

In addition to determining the portion of variation explained by the environmental variables, it is important to interpret the role of these variables in structuring communities. Although the above results appear to have ecological significance (e.g., see East and Magnan 1991; Tremblay and Magnan 1991; Lacasse and Magnan 1992), one must be cautious in interpreting the causal relationships between dependent and independent variables retained in the analysis. The latter are selected by a forward selection procedure on the basis of proportion of variance explained and statistical significance (ter Braak 1990a). Therefore, such an analysis should be viewed as preliminary to a mechanistic approach, providing support and guidance for the investigation of more realistic variables in mechanistic studies. The mechanistic approach, through field or laboratory experiments, has been proposed as the most promising one for addressing functional proximal relationships and enabling ecologists to better understand community patterns (Schoener 1986; Dill 1987; Persson and Diehl 1990). The use of this approach, however, requires some previous understanding of the potential key factors structuring a given system.

Even though our sampling strategy was not specifically designed to investigate the temporal component, results show that a temporal effect can be identified from our analysis; the date of sample collection has a significant effect on the trout diet, suggesting an influence of seasonality in resource availability or physiological requirements of the fish (e.g., temperature). In a study extending over a longer period in the summer season (May–August), Tremblay and Magnan (1991) showed that the niche shift of brook trout from littoral zone zoobenthos to pelagic prey was related to a decrease of food supply and an increase of temperature in the littoral zone.

The geographical coordinates and drainage pattern analyses showed that variation of trout diet composition among the 37 study lakes is spatially structured, i.e., that spatial variables explained an independent part of the diet variation after removal of the effect of measured environmental variables. In fact, the "pure" spatial component presumably reflects the effects of environmental variables that are spatially structured. The model based on geographic coordinates accounted for 30.4% of the total diet variation whereas the model based on drainage pattern accounted for 29.5%. Such a spatial structure could reflect phenotypic or genotypic differences in brook trout populations. Variation in diet explained by the drainage pattern may be the result of dispersal of introduced species in the different drainage subbasins. Another nonexclusive hypothesis is that variation in diet explained by the drainage pattern may be the result of

geographic isolation between brook trout in the different subbasins, which could have led to long-term genetic differentiation. In contrast, variation in diet explained by geographic coordinates could have been the result of the pattern of baitfish introductions by anglers in these lakes, although their further dispersal could have been affected by drainage pattern. Actually, chub and sucker introductions must have occurred in lakes that were accessible by roads; this, in turn, is more a function of geography than of drainage pattern. As it is known that phenotypic changes have occurred in brook trout morphology (gill rakers and pyloric caeca) following these introductions (Magnan 1988; Magnan and Stevens 1993), it is possible that spatial variation in trout diet is related to the pattern of fish introductions. Although it would have been possible to incorporate some measure of accessibility such as distance from the road in our statistical analyses, interpretation of results would have been complicated by the fact that the road network has changed a great deal during the last century, in response to forest exploitation. Thus, present accessibility does not necessarily reflect past accessibility.

It is also possible that for a given introduced species, the trout has been in contact with genetically different populations, leading to different phenotypic responses. If this is the case, trout response can be measurable today in terms of both the drainage and geographical coordinate variables. The two methods of quantifying spatial structure will not always be simultaneously useful, or applicable to a given system. However, the drainage pattern method should always be used in combination with geographic coordinates when there is a network of connections between the sampling sites because the two methods can be complementary; this is the case, for instance, for creeks and streams connecting the lakes in this study, for valley networks facilitating dispersal of insects (M. Dufrêne, personal communication), or for land bridges connecting islands to the mainland through geological history (MacArthur 1972; Magnuson 1976). In addition to giving the portion of total variation accounted for by the spatial structure and permitting tests of statistical significance, our method of analysis allows one to frame testable functional hypotheses about the ecological significance of the spatial component.

The analysis showed that one can partition the total variation of the dependent variables (here, trout diet composition) into four independent components, "pure" environmental, "pure" spatial, shared, and unexplained, by using the procedure of Borcard et al. (1992). An extension of this method also allowed us to partition the total dietary variation among three sets of explanatory variables (environmental, geographic coordinates, and drainage pattern). The two sets of spatial variables extracted different, largely nonoverlapping components of the dietary variation (Fig. 5). This part of the analysis is efficient because it allows for simultaneous consideration of sets of environmental (biotic and abiotic) and spatial variables to account for dependent variables such as species density or resource use at different sampling sites. For example, Lacasse and Magnan (1992) built seven multiple regression models to predict the mean percent weight of seven components of brook trout diet from different biotic and abiotic variables; these models accounted for between 25.9 and 88.0% of the variation of given food items in the fish diet, which represents for most food items an overestimation of the importance of the environmental variables in structuring trout diet, compared with the results presented here. This overestimation probably owes to the fact that they modelled each of the seven components of the diet as if they were independent when in fact they are correlated (ter Brack and Prentice 1988). Using the same diet data that had been analyzed by Lacasse and Magnan (1992), the present analysis shows that the addition of spatial variables and the consideration of all components of the diet simultaneously can yield a different picture. If individual dietary components do not respond to the same composite gradient of environmental variables, the use of several regression models instead of ordination may allow for more detailed descriptions of the response of each dietary component to environmental variation (ter Braak and Prentice 1988; Rodríguez et al. 1993). However, this increase in detail also implies that overall, more environmental variables have to be included in the analysis. The approach used by Lacasse and Magnan (1992) retained more than 15 different environmental variables as predictors in seven separate regression models; in contrast, only five environmental variables were retained by the selection procedure in the present study. Among the environmental variables, differences in fish species composition appeared to be the major determinant of trout diet in the two studies. Nevertheless, our results suggest that the approach used by Lacasse and Magnan (1992) may have overestimated the *overall* effect on the diet of certain littoral habitat characteristics (e.g., variables reflecting littoral occupation of rock outcrops or refuge quality), which appeared in five of their seven models, and underestimated that of pH and of trout length, which appeared in only one model each. The overlap between the environmental and spatial components (Fig. 5) also suggests that a substantial part of the environmental effects detected in Lacasse and Magnan's (1992) study may in fact be interpretable as historical effects related to fish introductions, or to neglected (unmeasured) environmental variables that covary in space with the measured environmental variables retained by the selection procedure. The inclusion of the spatial component in our study led to testable hypotheses concerning introductions and dispersal of fish species (see above); such hypotheses are unlikely to arise naturally from studies that consider only the effect of the environmental component.

Our analysis used diet composition of brook trout as the dependent variable. Other dependent variables, such as population density, resource use, morphometric characteristics, or genotypic frequencies of, e.g., birds species on islands and the mainland, or of fish species at different stations along a coral reef, could be used within the same statistical framework in community ecology studies.

Acknowledgments

We are thankful to D. Courtois, J.-F. Duchesne, N. Gélinas, S. Gour, E. Harnois, and L. Thiffeault for their appreciated field and laboratory assistance and to J. Archambault, C. Garceau, and M. Bellemare from the ministère de l'Environnement et de la Faune, Québec Government, for invaluable logistic support. Théophile Niyonsenga helped draw Fig. 5. This work was supported by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and le Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (FCAR), Québec Government, to P. Magnan and from le Groupe de recherche interuniversitaire en limnologie (GRIL) to P. Legendre and P. Magnan. S. Lacasse was supported by an NSERC postgraduate fellowship.

References

BENNETT, W.A. 1990. Scale of investigation and the detection of competition: an example from the house sparrow and house finch introductions in North America. Am. Nat. 135: 725–747.

BILBY, R.E., AND J.W. WARD. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Can. J. Fish. Aquat. Sci. 48: 2499–2508.

BORCARD, D., AND P. LEGENDRE. 1994. Environmental control and spatial structure in ecological communities: an example using Oribatid mites (Acari, Oribatei). Environ. Ecol. Stat. 1: 37–53.

BORCARD, D., P. LEGENDRE, AND P. DRAPEAU. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045–1055.

CARLANDER, K.D. 1969. Handbook of freshwater fishery biology. Vol. 1. Iowa State University Press, Ames, Iowa. 752 p.

DANIELSON, B.J. 1991. Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. Am. Nat. 138: 1105–1120.

DIAMOND, J.M. 1986. Overview: laboratory experiments, field experiments, and natural experiments, p. 3–22. *In* J. Diamond and T.J. Case [ed.] Community ecology. Harper & Row, New York, N.Y.

DILL, L.M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behavior. Can. J. Zool. 65: 803–811.

DUNSON, W.A., AND J. TRAVIS. 1991. The role of abiotic factors in community organization. Am. Nat. 138: 1067–1091.

EAST, P., AND P. MAGNAN. 1991. Some factors regulating the piscivory of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. Can. J. Fish. Aquat. Sci. 48: 1735–1743.

GAUCH, H.G. JR. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York, N.Y.

HART, D.D. 1992. Community organization in streams: the importance of species interactions, physical factors, and chance. Oecologia 91: 220–228.

HYSLOP, E.J. 1980. Stomach contents analysis — A review of methods and their application. J. Fish Biol. 17: 411–429.

JACKSON, D.A., K.M. SOMERS, AND H.H. HARVEY. 1992. Null models and fish communities: evidence of nonrandom patterns. Am. Nat. 139: 930–951.

KLUGE, A.G., AND J.S. FARRIS. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18: 1–32.

LACASSE, S., AND P. MAGNAN. 1992. Biotic and abiotic determinants of the diet of brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. Can. J. Fish. Aquat. Sci. 49: 1001–1009.

LACASSE, S., AND P. MAGNAN. 1994. Distribution post-glaciaire de l'omble de fontaine dans le bassin hydrographique du fleuve Saint-Laurent: impact des interventions humaines. Université du Québec à Trois-Rivères (Québec) Canada pour le ministère de l'Environnement et de la Faune du Québec. Rapp. tech. 83 p.

LACHANCE, S., AND P. MAGNAN. 1990a. Performance of domestic, hybrid, and wild strains of brook trout, *Salvelinus fontinalis*, after stocking: the impact of intra- and interspecific competition. Can. J. Fish. Aquat. Sci. 47: 2278–2284.

LACHANCE, S., AND P. MAGNAN. 1990b. Comparative ecology and reproductive potential of domestic, hybrid, and wild strains of brook trout, *Salvelinus fontinalis*, after stocking. Can. J. Fish. Aquat. Sci. 47: 2285–2292.

LEGENDRE, P. 1990. Quantitative methods and biogeographic analysis, p. 9–34. *In* D.J. Garbary and G.R. South [ed.] Evolutionary biogeography of the marine algae of the North Atlantic. NATO ASI Series. Vol. 22. Springer-Verlag, Berlin, Germany.

LEGENDRE, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74: 1659–1673.

LEGENDRE, L., AND P. LEGENDRE. 1983. Numerical ecology. Developments in environmental modelling, 3. Elsevier, Amsterdam, The Netherlands.

LEGENDRE, P., AND M. TROUSSELLIER. 1988. Aquatic heterotrophic bacteria: modeling in the presence of spatial autocorrelation. Limnol. Oceanogr. 33: 1055–1067.

MACARTHUR, R.H. 1972. Geographical ecology, patterns in the distribution of species. Harper & Row, New York, N.Y.

MAGNAN, P. 1988. Interactions between brook charr, *Salvelinus fontinalis*, and nonsalmonid species: ecological shift, morphological shift, and their impact on zooplankton communities. Can. J. Fish. Aquat. Sci. 45: 999–1009.

MAGNAN, P. 1989. The impact of cyprinid and catostomid introductions on brook char, *Salvelinus fontinalis*, populations: a review. Physiol. Ecol. Jpn. 1989: 337–356.

MAGNAN, P., AND G.J. FITZGERALD. 1982. Resource partitioning between brook trout, *Salvelinus fontinalis* Mitchill, and creek chub, *Semotilus atromaculatus* Mitchill, in selected oligotrophic lakes of southern Québec. Can. J. Zool. 60: 1612–1617.

MAGNAN, P., AND G.J. FITZGERALD. 1984a. Ontogenetic changes in diel activity, food habits and spatial distribution of juvenile and adult creek chub, *Semotilus atromaculatus*. Environ. Biol. Fishes 11: 301–307.

MAGNAN, P., AND G.J. FITZGERALD. 1984b. Mechanisms responsible for the niche shift of brook charr, *Salvelinus fontinalis* Mitchill, when living sympatrically with creek chub, *Semotilus atromaculatus* Mitchill. Can. J. Zool. 62: 1548–1555.

MAGNAN, P., AND E.D. STEVENS. 1992. Pyloric caecal morphology of brook charr, *Salvelinus fontinalis*, in relation to diet. Environ. Biol. Fishes 36: 205–210.

MAGNUSON, J.J. 1976. Managing with exotics — a game of chance. Trans. Am. Fish. Soc. 105: 1–9.

MENGE, B.A., AND A.M. OLSON. 1990. Role of scale and environmental factors in regulation of community structure. Trends Ecol. Evol. 5: 52–57.

MONTGOMERY, D.C., AND E.A. PECK. 1982. Introduction to linear regression analysis. Wiley, New York, N.Y. 504 p.

NAUD, M., AND P. MAGNAN. 1988. Diel onshore–offshore migrations in northern redbelly dace, *Phoxinus eos*. Can. J. Zool. 66: 1249–1253.

NORTON, S.F. 1991. Habitat use and community structure in an assemblage of cottid fishes. Ecology 72: 2181–2192.

PERSSON, L., AND S. DIEHL. 1990. Mechanistic individual-based approaches in the population/community ecology of fishes. Ann. Zool. Fenn. 27: 165–182.

PIELOU, E.C. 1984. The interpretation of ecological data. A primer on classification and ordination. Wiley, New York, N.Y.

RICKLEFS, R.E. 1987. Community diversity: relative roles of local and regional processes. Science (Wash., D.C.) 235: 167–171.

RODRÍGUEZ, M.A., AND P. MAGNAN. 1993. Community structure of lacustrine macrobenthos: do taxon-based and size-based approaches yield similar insights? Can. J. Fish. Aquat. Sci. 50: 800–815.

RODRÍGUEZ, M.A., P. MAGNAN, AND S. LACASSE. 1993. Fish species composition and lake abiotic variables in relation to the abundance and size structure of cladoceran zooplankton. Can. J. Fish. Aquat. Sci. 50: 638–647.

SALE, P.F. 1979. Habitat partitioning and competition in fish communities, p. 323–331. *In* R.H. Stroud and H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, D.C.

SCHOENER, T.W. 1982. The controversy over interspecific competition. Am. Sci. 70: 586–595.

SCHOENER, T.W. 1986. Mechanistic approaches to community ecology: a new reductionism ? Am. Zool. 26: 81–106.

SCOTT, W.B., AND E.J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

TER BRAAK, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis in ecology. Ecology 67: 1167–1179.

TER BRAAK, C.J.F. 1987. Ordination, p. 91–173. *In* R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. van Tongeren [ed.] Data analysis in community and landscape ecology. Pudoc, Wageningen, The Netherlands.

TER BRAAK, C.J.F. 1988a. Partial canonical correspondence analysis, p. 551–558. *In* H.H. Block [ed.] Classification and related methods of data analysis. North Holland Press, Amsterdam, The Netherlands.

TER BRAAK, C.J.F. 1988b. CANOCO — an extension of DECORANA to analyze species–environment relationships. Vegetatio 75: 159–160.

TER BRAAK, C.J.F. 1990a. Update notes: CANOCO version 3.10. Agricultural Mathematics Group, Wageningen, The Netherlands. (Mimeo.)

TER BRAAK, C.J.F. 1990b. Interpreting canonical correlation analysis through biplots of structural correlations and weights. Psychometrika 55: 519–531.

TER BRAAK, C.J.F., AND I.C. PRENTICE. 1988. A theory of gradient analysis. Adv. Ecol. Res. 18: 271–317.

TREMBLAY, S., AND P. MAGNAN. 1991. Interactions between two distantly related species, brook trout, *Salvelinus fontinalis*, and white sucker, *Catostomus commersoni*. Can. J. Fish. Aquat. Sci. 48: 857–867.

VENNE, H., AND P. MAGNAN. 1995. The impact of intra- and interspecific interactions on young-of-the-year brook charr, in temperate lakes. J. Fish Biol. 46. (In press)

WILKINSON, L. 1990. SYSTAT: a system for statistics. SYSTAT Inc., Evanston, Ill.

WISMER, D.A., AND A.E. CHRISTIE. 1987. Temperature relationships of Great Lakes fishes: a data compilation. Great Lakes Fish. Comm. Spec. Publ. No. 87-3: 195 p.

Development and Effect of Female Size on Egg and Juvenile Production in the Neogastropod *Buccinum cyaneum* from the Saguenay Fjord

Patricia Miloslavich[1] and Louise Dufresne

Département d'Océanographie, Université du Québec, 310 allée des Ursulines, Rimouski, QC G5L 3A1, Canada

Miloslavich, P., and L. Dufresne. 1994. Development and effect of female size on egg and juvenile production in the neogastropod *Buccinum cyaneum* from the Saguenay Fjord. Can. J. Fish. Aquat. Sci. 51: 2866–2872.

The size at sexual maturity, the developmental timing and biology, and the biochemical (protein, glycogen, and lipid) content of eggs and juveniles were determined in two female size groups of the buccinid *Buccinum cyaneum*. Males reach sexual maturity at a smaller size (27 mm in shell length) than females (37 mm). A total of 33 females spawned in the laboratory starting in November 1991. The egg capsules were concave, measured 6.3 mm in diameter, and contained between 300 and 1000 eggs measuring 240 μm in diameter. Between 1 and 10 embryos developed. The others underwent chromatin degeneration within 3–4 wk and became nurse eggs. Between 1 and 10 crawling juveniles emerged 9 mo later in July and August and measured 2.5 ± 0.3 mm in shell length. The number of eggs and developing embryos within egg capsules increased with the size of the female. However, the quality of the juvenile at hatching, both in size and in biochemical content, did not vary significantly with female size.

On a déterminé la taille à la maturité sexuelle ainsi que la chronologie et al biologie du développement et le contenu biochimique (protéines, glycogène et lipides) des oeufs et des juvéniles produits par deux groupes de femelles de tailles différentes chez le buccinidé *Buccinum cyaneum*. L'atteinte de la maturité sexuelle a lieu chez les mâles à une taille plus petite (longueur de la coquille de 27 mm) que chez les femelles (37 mm). La ponte des 33 femelles au laboratoire a débuté en novembre 1991. Les oothèques étaient concaves, leur diamètre était de 6,3 mm et elles contenaient de 300 à 1 000 oeufs dont le diamètre était de 240 μm. Dans chacune, de 1 à 10 embryons se sont développés alors que les autres oeufs ont connu une dégénération de leur chromatine dans leurs 3–4 premières sem et sont devenus des oeufs nourriciers. De 1 à 10 juvéniles ont émergé 9 mo plus tard, en juillet et en août, et la longueur de leur coquille était alors de 2,5 ± 0,3 mm. Le nombre d'oeufs et d'embryons qui se sont développés dans les oothèques variaient en raison directe de la taille des femelles. Toutefois, la taille et le contenu biochimique des juvéniles à l'éclosion ne variaient pas de façon significative selon la taille des femelles.

Received September 27, 1993
Accepted May 30, 1994
(J12106)

Reçu le 27 septembre 1993
Accepté le 30 mai 1994

The reproductive biology in the family Buccinidae has long been a subject of research. Portmann (1925, 1930) described for the first time the embryology of *Buccinum undatum*; Lamy (1928) described the morphology of egg capsules belonging to *B. undatum*, *B. humphreysianum*, *B.* cf. *cyaneum*, and *B. glaciale* (*B. angulosum*). Thorson (1935) studied the egg capsules of *B. hydrophanum*, *B. belcheri*, *B. groenlandicum*, *B. sericatum*, and *B. ovum*. Staiger (1951) and Fioroni and Schmekel (1976) have added valuable information dealing with cytology, morphology, and ontogenesis of *B. undatum*.

In the Gulf of Saint Lawrence, eastern Canada, the behaviour, timing of copulation, reproductive cycle, and biology of *B. undatum* have been thoroughly studied (Martel et al. 1986a, 1986b; Gendron 1990; Himmelman and Hamel 1993). This is a commercially valuable resource, and due to overfishing, some stocks have been depleted and have not recovered (Gendron 1990). To implement a management strategy, Gendron (1990, 1992) determined the size and age at sexual maturity to aid in establishing an appropiate minimum catchable size. She found that the size at sexual maturity varied among populations within the Gulf. The question therefore arises whether the quantity or quality of the brood stock depends on female size.

There are several papers dealing with the relation of clutch size to female size (Smith and Fretwell 1974; Spight et al. 1974; Spight 1976a, 1976b; Spight and Emlen 1976). In the family Muricidae, Spight et al. (1974) concluded that larger females deposit larger egg capsules than small females and these capsules contain more eggs. If a management strategy to protect stocks from overfishing is to be established, these parameters should be taken into account.

Biochemical studies on developing embryos of gastropods have been undertaken by Morrill (1973) in the pulmonate *Physa fontinalis* and by Deslous-Paoli and Héral (1986) in *Crepidula fornicata*, showing in both cases the increase in the biochemical content from the egg to the hatching stage.

Buccinum cyaneum is an abundant benthic invertebrate at the Saguenay Fjord, and contrary to *B. undatum*, its reproductive biology remains unknown. In this paper the developmental

[1]Present address: Universidad Simón Bolívar, Departamento de Estudios Ambientales, Apartado Postal 89.000, Caracas 1080, Venezuela.

kinetics and biochemistry of *B. cyaneum* are described. The reproductive effort in terms of size and biochemical content of the different stages of development in relation to female size were also measured.

Materials and Methods

Specimens

Buccinum cyaneum (Bruguière 1792): material from this study has been deposited in the Harvard Museum of Comparative Zoology under catalogue No. MCZ 302636.

Buccinum cyaneum were collected in July 1991, between 20 and 40 m in depth from the southwest side of the Anse St. Jean, Saguenay Fjord, Quebec, Canada, with the help of baited cages. Specimens were kept in troughs at the Pointe-au-Père Aquaculture Station and supplied with seawater pumped in from the St. Lawrence Estuary. The temperature varied from 5 to 10°C and salinities from 28 to 32 ppt. They were frozen fish fed twice a week.

An anatomical study of the gonad was made of 170 whelks to determine the size at sexual maturity. Males with a well-developed seminal vesicle containing sperm and females with a large yellow gonad containing many ovocites were considered sexually mature. Sexually mature females were classified in two groups according to shell length. The first group ranged from 35 to 49 mm in length, and the second consisted of all females larger than 50 mm.

Development under Laboratory Conditions

A total of 33 spawnings were obtained in the laboratory. The following aspects were studied: number and size of egg capsules spawned per female, number and size of eggs and developing embryos within the capsule, identification of the stages of development, and time of development from egg to hatching.

The egg masses were kept in the troughs with the same conditions as the adults. During the first week after egg laying, one capsule from each female was sampled daily. Subsequently, two capsules were taken from each female each week until the embryos reached an early prehatching stage (no velar remnants, well-developed foot and siphon, early calcified shell). At this stage, three to four capsules were sampled twice a week until hatching. The observations were made on living material.

The eggs and embryos were fixed in a glucamine–acetate (GA) buffer containining 4–6% formalin for 12 h. This buffer was prepared with 250 mM *N*-methyl glucamine, 250 mM potassium gluconate, 50 mM HEPES, and 10 mM EGTA. The pH was adjusted to 7.4 with acetic acid. After fixation, the material was rinsed twice with GA buffer and a third time with GA buffer containing 0.5 μg fluorochrome Hoechst 33258/mL which is a specific stain for the DNA. After 30–60 min, the samples were rinsed twice with GA buffer. Observations were carried out with a Leitz MPV 3 epifluorescence microscope equipped with appropiate filters for Hoechst fluorescent probes.

Biochemical Procedures

Coincident with the sampling done for developmental kinetics, part of the material was flash-frozen alive in 1.5 mL of eppendorfs at −20°C for protein, glycogen, and lipid analysis of the eggs, embryos, larvae, and juveniles.

Protein was determined following the Bio-Rad protein microassay procedure based on the Bradford method. Bovine serum albumin was used as a standard. Samples were left overnight in 0.5 N NaOH and thoroughly homogenized.

Glycogen was determined by a modification of the Dreiling et al. (1987) method. The procedure consists of extraction of glycogen with 10% perchloric acid (PCA) and iodine-binding to produce colour. Mussel VII glycogen (Sigma) was used as a standard. Samples in 1.5 mL of eppendorfs were left overnight with 1.2 mL of 10% PCA and then homogenized by vortexing and with the help of a micropipet. Samples were then centrifuged for 2 min at 30 000 rpm and the supernatant saved for glycogen determination. The pellets were reextracted twice with 0.6 mL of 10%. For spectrophotometer readings, 0.2 mL of the supernatants was combined with 0.8 mL of the iodine colour reagent. The reagent was prepared by combining 1.3 mL of a solution containing 0.26 g of iodine and 2.6 g of potassium iodide (in 10 mL of distilled water, fresh daily) with 100 mL of saturated $CaCl_2$. Absorbance measurements were made after 10–30 min at 460 nm using 0.2 mL of PCA plus 0.8 mL of reagent as a blank. The quantity of glycogen per sample was obtained by adding the results of the three extractions.

The lipid assay was done by modifying the methods of Bligh and Dyer (1959) and Barnes and Blackstock (1973). Olive oil (10 mg/mL in chloroform) was used as a standard. Samples in 1.5 mL of eppendorfs were homogeneized with 1 mL of a mixture of chloroform–methanol (2:1, v/v) and centrifuged for 10–15 s at 30 000 rpm. The supernatant was saved in a dry Pyrex test tube. The pellets were reextracted twice with 1 mL of the mixture. All supernatants were saved and filtered together through a No. 1 Whatman filter into a 10-mL dry Pyrex tube with a cap. The filter paper and test tube were rinsed with 3 mL of the solvent mixture, and 2 mL of a 9% aqueous solution of NaCl was added, mixed gently, and left overnight at 2°C. The lower, organic phase was collected in a 50-mL volumetric flask and the volume made up to 50 mL with chloroform. From the solution, 0.5 mL was transferred to a dry Pyrex test tube with a cap and evaporated to dryness with nitrogen gas. To the residue, 0.5 mL of concentrated sulphuric acid was added, mixed gently, and heated in a boiling water bath for 10 min with the test tube caps loosened. After cooling, 2.5 mL of a phosphovanillan reagent (0.2 g of vanillan in a 80% aqueous solution of orthophosphoric acid) was added to the tube and mixed. Absorbance was read after 50 min at 520 nm with a chloroform blank. All optical density readings were made on a Perkin-Elmer UV/VIS spectrophotometer Lambda 3, series 37573.

Results

Males attained sexual maturity at a significantly smaller size (*t*-test: $p < 0.001$) than females (males: minimal = 27.5 mm, mean 36.8 ± 2.9 SD, $n = 47$; females: minimal = 38.5 mm, mean 50.2 ± 5.7 SD, $n = 21$).

Development

Females spawned on hard substrates, preferring vertical surfaces (such as glass and the walls of the troughs). No communal behaviour was observed in spawning females in the laboratory. Furthermore, these females used their proboscis to keep other whelks away from their spawn. Some females

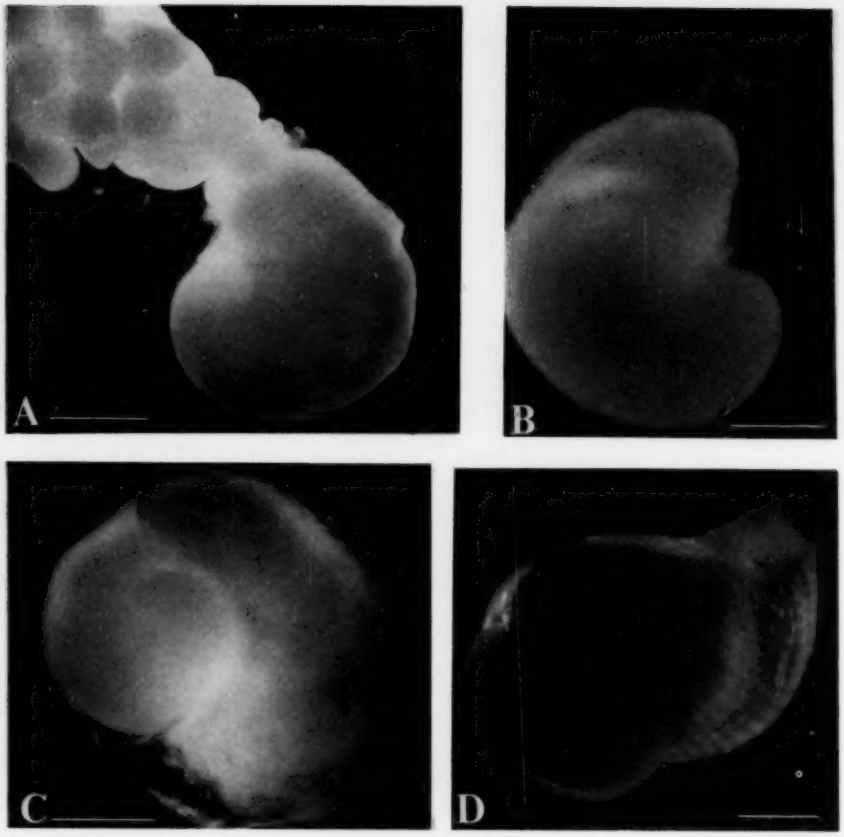


FIG. 1. Development of *Buccinum cyaneum*. (A) Embryo attached to the nurse egg mass; (B) development of the small velum; (C) pediveliger stage; (D) hatching stage. Scale bar = 500 μm.

were observed to abandon their spawns to feed and return afterwards. Laying of egg capsules began in November 1991; the mean number of egg capsules laid per female was 101 (SD = ±22, n = 26). These capsules were concave and had a mean size of 6.3 mm (SD = ±0.7, n = 226; size was measured as the average of the capsule's height and width). The egg capsules covering the exterior of the mass contained from 40–50 to 0 eggs. The interior capsules contained 567 ± 227 (n = 76) eggs with a mean diameter of 240 ± 21.5 μm.

Observations of the eggs under fluorescent light showed the emission of the two polar bodies after fertilization and prior to nuclear fusion. Due to the enormous amount of vitelus in the egg, we were unable to determine the exact egg maturation stage at the time of sperm entry, but we suspect that it was at the stage of primary oocyte or the meiois I prophase, as we observed eggs at this stage with the intact sperm in the interior. Follicular cells were not observed in any eggs.

The first division leading to the two-cell stage occurred within the first 24 h, but few eggs entered this stage. Some eggs remained at the primary oocyte stage with the sperm in the interior, and some showed no signs of either sperm or female chromatin condensation. Between 0.18 and 1.8% of the eggs completed their development to hatching; the rest became nurse eggs, which were ingested by the developing embryos. Ingestion of nurse eggs began in March, the embryos attaching themselves to the nurse egg mass and swallowing them intact (Fig. 1A). In April, all nurse eggs were totally ingested and the embryos measured around 1.5 mm in maximal length. Observations of the nurse egg under fluorescent light showed that the chromatin of the nurse egg degenerated 3–4 wk after egg-laying. Other eggs underwent abnormal cleavage and developed no further.

In May 1992, the intracapsular veliger stage was reached. This veliger measured around 2.0 mm in shell length. The velum was small and rounded in shape and the shell was transparent yellow and very fragile (Fig. 1B). This veliger was unable to swim. Between June and July, a foot developed. The shell of this pediveliger stage measured 1.9 mm in length and was still fragile (Fig. 1C). In July, the velum had completely dissappeared, the foot and mantle showed some pigmentation, and the shell had begun to darken. The shell of this prehatching stage measured around 2.1 mm in length. In July–August, crawling juveniles had hatched, the foot, mantle, and head had black spot pigmentation, and the shell had reddish pigmentation and measured 2.5 mm (SD = ±0.33 mm) (Fig. 1D). There were between 1 and 10 hatchlings

TABLE 1. Development of *Buccinum cyaneum* under laboratory conditions. Numbers in parentheses indicate range.

Stage	Time (mo) and month	Embryo size (mm) (mean ± SD)
Egg	0 November	0.24 ± 0.02 (0.22–0.32) n = 265
Embryo (all nurse eggs ingested)	5 April	1.52 ± 0.29 (0.86–2.30) n = 204
Intracapsular veliger	6 May	2.00 ± 0.23 (1.51–2.23) n = 9
Intracapsular pediveliger	6.5–7 June–July	1.89 ± 0.26 (1.26–2.52) n = 73
Prehatching	7–7.5 July	2.15 ± 0.29 (1.62–2.88) n = 76
Hatching	8 August	2.46 ± 0.33 (1.62–3.96) n = 182

per capsule (2.7 ± 1.9; n = 83). The juveniles escaped from the egg capsule by a preformed plug that dissolved prior to hatching (Table 1).

In December 1992, 4 mo after hatching, the benthic juveniles had grown to a shell length of 3.7 ± 0.7 mm (n = 26, maximal length 5.2 mm).

Female Shell Length – Spawning Relations

Female shell length (40–56 mm) was directly correlated with egg capsule size, reported as the mean between height and width (Pearson correlation coefficient: $p < 0.01$; Fig. 2A). The number of eggs deposited in each capsule and the number of developing embryos (juveniles at hatching) were also significantly correlated with female shell length (Pearson correlation coefficient: $p < 0.01$ and $p < 0.01$, respectively; Fig 2B and 2C). The shell length of the juveniles (2.46 ± 0.33 mm, n = 182) at hatching showed no correlation with female shell length (Pearson correlation coefficient: $p > 0.01$), which means that the size of the juvenile did not depend on female size (Fig. 2D).

A size comparison between juveniles coming from egg capsules containing one, two, three, four, and five or more hatchlings was done. Results indicated that juveniles that developed in egg capsules with one single hatchling (2.64 ± 0.4 mm in shell length, n = 25) are significantly larger than those that developed in egg capsules with five or more hatchlings (2.25 ± 0.3 mm in shell length; t-test: $p < 0.01$). We found no significant differences in the size of the juveniles that developed in egg capsules with two, three, and four hatchlings (t-test: $p > 0.01$), but there is a tendency towards an increase in size in juveniles that developed alone or with fewer capsulemates.

Biochemical Content

During development, between the egg stage and the intracapsular veliger stage, the protein, glycogen, and lipid content of the individuals within the egg capsules increased and then remained almost unchanged until the hatching stage

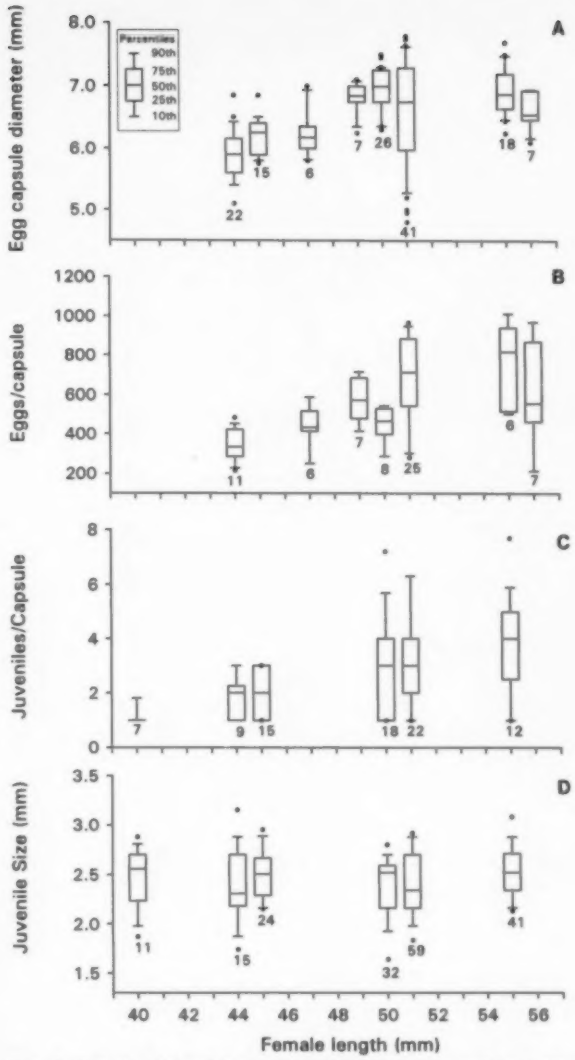


FIG. 2. Relationship of female shell length to egg and juvenile. (A) Egg capsule size is the mean between height and width; (B) mean number of eggs per capsule; (C) mean number of juveniles per capsule; (D) juvenile size. Vertical bars indicate the 95% confidence interval for the mean. Numbers associated with bars indicate the number of observations.

(ANOVA followed by Tukey multiple comparisons: $p < 0.01$). This period included the nurse egg ingestion. Once all the nurse eggs had been ingested, protein, glycogen, and lipid content changed little (Table 2).

As there were no differences in size between the juveniles of *B. cyaneum*, for the biochemical analysis, these were divided into two groups according to the shell length of the female (group 1: less than 50 mm; group 2: 50 mm and larger; 50 mm = mean size at sexual maturity). There were no significant differences in the protein, glycogen, and lipid content of the juveniles (Mann–Whitney U-test: $p > 0.05$) between the two groups, indicating that the biochemical quality of the juvenile did not depend on female size (Fig. 3).

TABLE 2. Protein, glycogen, and lipid content (μg/individual) of *Buccinum cyaneum* embryos at the different developmental stages. Numbers in parentheses indicate range.

Stage	Protein	Glygogen	Lipid
Egg	2.2 ± 0.7 (1.1–3.2) n = 17	2.1 ± 1.4 (0.02–5.8) n = 18	2.9 ± 2.2 (0.4–7.7) n = 16
Pediveliger	240.4 ± 102.2 (98.4–343.2) n = 5	473.2 ± 102.2 (348.3–574.8) n = 5	232.0 ± 119.9 (93.6–437.5) n = 8
Prehatching	270.8 ± 87.4 (143.2–331.3) n = 4	581.4 ± 288.6 (252.2–918.5) n = 4	236.1 ± 144.0 (120.1–483.1) n = 5
Hatching	289.0 ± 175.4 (91.2–672) n = 11	534.5 ± 151.5 (335.1–777.0) n = 11	249.4 ± 152.3 (36.1–635.8) n = 17

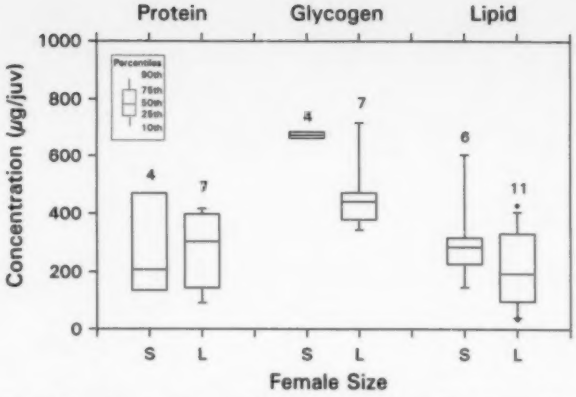


FIG. 3. Protein, glycogen, and lipid content of juveniles of two different female shell length groups. Group 1: females smaller than 50 mm; group 2: females 50 mm and larger.

Discussion

Development

A common feature of *Buccinum* species is that many eggs do not develop and are ingested by the developing embryos as nurse eggs (Portmann 1925, 1930; Lamy 1928; Thorson 1935; Staiger 1951; Fioroni and Schmekel 1976). In *B. cyaneum*, only 0.2–1.8% of the eggs complete development. The nurse eggs undergo chromatin degeneration beginning 3–4 wk after egg-laying, and in some, this degeneration occurs up to 2 mo after egg-laying, a phenomenon that has not been previously reported. Staiger (1951) reported that only 1% of the eggs of *B. undatum* undergo normal development, 75% of the eggs are fertilized but stop development at metaphase of the first maturation division, and 24% of the eggs complete the first maturation division but develop no further. Hyman (1935) reported that in nurse eggs of *Fasciolaria tulipa*, the chromosomes form vesicles that remain near the center of the egg until it is swallowed by the veliger. What determines the origin of the nurse eggs is poorly understood. Hypotheses attempting to explain the production of nurse cells were reviewed by Webber (1977); such hypotheses involve abnormal spermatozoa (Hyman 1935 for *F. tulipa*) and possible genetic factors in the egg (Staiger 1951 for *B. undatum*). West (1979) indicated that in the buccinid *Colus stimpsoni*, nurse eggs are not a result of fertilization by atypical sperm, but rather the result of normally fertilized eggs which are defective or lack factors that trigger or control zygote cytokinesis.

Buccinum cyaneum is similar to *B. undatum* in that it surrounds its spawn masses with capsules which contain few or no eggs. This is probably a defense mechanism against predators such as sea urchins. The interior capsules of both species have approximately the same proportion of nurse eggs to developing embryos, although *B. undatum* deposits twice as many eggs per capsule (Martel et al. 1986a). Egg diameter and hatching size are similar for the two species, and in both, crawling juveniles emerge from the capsules. *Buccinum cyaneum* deposits its capsules (under laboratory conditions) in November and *B. undatum* in June–July (Martel 1986a; Himmelman and Hamel 1993). The developmental period is 3 mo longer in *B. cyaneum* and the nurse eggs are totally consumed by the developing embryos by the fourth month in *B. cyaneum* compared with the third week in *B. undatum*. This delay in *B. cyaneum* in the Saguenay could be either genetically determined or the result of environmental conditions in the Saguenay. The Saguenay Fjord has physical and chemical features which are characteristic of the arctic region (Schafer et al. 1990).

Differences in the reproduction in relation to biogeographic range have been reported by Hain and Arnaud (1992). These authors concluded for high-Antarctic gastropods that, in comparison with related temperate species, egg sizes are up to four times larger and the embryonic development is up to 30 times longer. For example, from the egg capsules of the buccinid *Neobuccinum eatoni*, only one juvenile measuring 7.5 mm in shell length hatches. This shell is much larger than those of temperate buccinids, but the diameter of the egg and the number of eggs per capsule of this species have not been reported.

The *Buccinanops* species (also classified as Dorsaninae and Nasaridae) studied by Penchaszadeh (1971a, 1971b, 1973) in the temperate Atlantic coast of South America also share features with the North American buccinids. These also produce egg capsules, nurse eggs are present, the number of developing embryos (between 1 and 10) is similar, and crawling juveniles emerge from the capsules. They differ in several aspects; firstly, the egg capsules are attached to the callous region of the shell of the parent, and the nurse eggs are arranged in aggregates surrounded by a thin membrane. Secondly, the size of the egg (up tp 400 μm) and the size at hatching (up to 7 mm) are greater than for *Buccinum* species. Finally, the ratio of embryos to nurse eggs is larger, which permits the embryo to attain a larger size.

Female Size – Spawning Relations

Our findings suggest that egg capsule size, number of eggs per capsule, and number of developing embryos are dependant on female size. This is consistent with Spight et al.'s (1974) results for murices. However, in the case of *B. cyaneum*, egg size and hatching size are not related to female size. Spight (1976a), studying *Thais emarginata* and *Acanthina spirata*, stated that prosobranch embryos feeding on nurse eggs often reach variable hatching sizes. Such variability could be due to an irregular distribution of the

eggs among the capsules. We found that the hatching size does not vary with the size of the female producing them. Furthermore, within a female size group, there is some variability in the hatching size that is related to the number of juveniles that will hatch from the egg capsule. As Spight (1976a) stated, the factors leading to hatching size variations are of substantial importance to the snails. In the case of *B. cyaneum*, however, female size does not seem to be one of these factors.

Biochemical Content

Our data show no significant changes in biochemical content during the last stages of development (the last 3 mo). The major increase in biochemical content occurs between the egg stage and the larva stage, which is the period of nurse egg ingestion. Once all the nurse eggs have been swallowed, the biochemical content is stable. This indicates that the only extra embryonic food source for the developing embryos is nurse eggs.

In *B. undatum* from the Gulf of St. Lawrence, we have observed an increase in the protein content from the egg stage (3.03 μg/egg) to the embryo stage (361.2 μg/embryo) and then a slow decrease to the hatching stage (106.8 μg/juvenile) (unpublished data). We observed a similar relationship for glycogen (5.43 μg/egg; 1076.6 μg/embryo; 830.96 μg/juvenile) but not for lipids (1.6 μg/egg; 1230.06 μg/embryo; 1512.03 μg/juvenile). The increase in protein and glycogen content to the embryo stage and slow decrease to the hatching stage seem to indicate that *B. undatum* juveniles consume more of their reserves during the intracapsular development than juveniles of *B. cyaneum*.

Morrill (1973) found in the pulmonate *P. fontinalis* a marked increase through development in the protein content beginning with 1 μg/egg to the 13-μg "head-pigmented" embryo stage 7 d later and then a slight decrease to 10.5 μg at the hatching stage 1 d later. These values are much lower than those reported for *B. cyaneum* and *B. undatum*. Biochemical changes during development have been discussed by Holland (1978), but this discussion concerned free-swimming larvae and not a restrained development within an egg capsule. In any case, his evidence supports the thesis that lipid rather than carbohydrate is the major metabolic energy reserve in most marine animals.

The biochemical determinations of *B. cyaneum* juveniles indicate that their protein, glycogen, and lipid content do not depend on the size of the female that produced them. However, there is an immense variability in the glycogen content of the juveniles produced by large females. The results of this work indicate that even when *B. cyaneum* is not commercially fished, a reduction in the number of large females due to overfishing would reduce the number of individuals produced but not affect their size or biochemical content. In other words, the impact of overfishing of *B. cyaneum* will not affect the quality of the brood stock in terms of the biochemical reserves or size of the juveniles, but it will certainly affect the quantity of individuals produced or brood size.

Acknowledgements

We wish to thank Dr. Bernard St. Marie of the Maurice Lamontagne Institute, Department of Fisheries and Oceans, for collecting the specimens at the Saguenay Fjord, Lucie Bossé for helping with the identification of the specimens, and Louise Gendron for her valuable information on buccinids. Special thanks go to Dr. John Himmelman of the Département de Biologie et GIROQ, Université Laval, for reviewing the manuscript. We are indebted to Dr. Silvard Kool of the Harvard Museum of Comparative Zoology for identifying the species. We also wish to thank Dr. Pablo Penchaszadeh and Eduardo Klein of the Universidad Simón Bolívar, Caracas, for their useful comments and suggestions for improving the manuscript and the Unidad de Medios Audiovisuales of the USB for their help with the photographs. This work was supported by a FIR–UQAR and CRSNG grant to Louise Dufresne and by a UQAR scholarship to Patricia Miloslavich.

References

Barnes, H., and J. Blackstock. 1973. Estimation of lipids in marine animals and tissues: detailed investigation of the sulphophosphovanillin method for total lipids. J. Exp. Mar. Biol. Ecol. 12: 103–118.

Bligh, E.G., and W.J. Dyer. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911–917.

Deslous-Paoli, J.M., and M. Héral. 1986. *Crepidula fornicata* L. (Gastéropode, Calyptraeidae) dans le bassin de Marennes-Oléron: composition et valeur énergétique des individus et des pontes. Oceanol. Acta 9: 305–311.

Dreiling, C.E., C.E. Brown, L. Casale, and L. Kelly. 1987. Muscle glycogen: comparison of iodine binding and enzyme digestion assays and application to meat samples. Meat Sci. 20: 167–177.

Fioroni, P., and L. Schmekel [ed.] 1976. Ontogeneses of gastropods with rich nutritive resources. Zool. Jahrb. Anat. Bd. 96: 74–171.

Gendron, L. 1990. Reproductive biology of the whelk *Buccinum undatum* in the Gulf of St. Lawrence: size and age at sexual maturity. ICES 1990 Shellfish Symp. No. 151.

Gendron, L. 1992. Determination of the size at sexual maturity of the waved whelk *Buccinum undatum* Linnaeus 1758 in the Gulf of Saint Lawrence as a basis for the establishment of a minimal catchable size. J. Shellfish Res. 11: 1–7.

Hain, S., and P.M. Arnaud. 1992. Notes on the reproduction of high-Antarctic molluscs from the Weddell Sea. Polar Biol. 12(578): 1–10.

Himmelman, J.H., and J.F. Hamel. 1993. Diet, behaviour and reproduction of the whelk *Buccinum undatum* in the northern Gulf of Saint Lawrence, eastern Canada. Mar. Biol. 116: 423–430.

Holland, D.L. 1978. Lipid reserves and energy metabolism in the larvae of benthic marine invertebrates, p. 85–123. *In* D.C. Malins and J.R. Sargent [ed.] Biochemical and biophysical perspectives in marine biology. Vol. 4. Academic Press, New York, N.Y.

Hyman, O.W. 1935. Natural partial fertilization in *Fasciolaria tulipa*. J. Morphol. 41: 267–281.

Lamy, E. 1928. La ponte chez les gastéropodes prosobranches. J. Conchyliol. Sér. 4, T. 26(72): 80–126.

Martel, A., D.H. Larrivée, and J.H. Himmelman. 1986a. Behaviour and timing of copulation and egg laying in the neogastropod *Buccinum undatum* L. J. Exp. Mar. Biol. Ecol. 96: 27–42.

Martel, A., D.H. Larrivée, K.R. Klein, and J.H. Himmelman. 1986b. Reproductive cycle and seasonal feeding activity of the neogastropod *Buccinum undatum*. Mar. Biol. 92: 211–221.

Morrill, J.B. 1973. Biochemical and electrophoretic analysis of acid and alkaline phosphatase activity in the developing embryo of *Physa fontinalis* (Gastropoda, Pulmonata). Acta Embryol. Exp. 61–82.

Penchaszadeh, P.E. 1971a. Observaciones sobre la reproducción y ecología de *Dorsanum moniliferum* (Valenciennes, 1834) (Gastropoda, Buccinidae) en la región de Mar del Plata. Neotropica 17(53), 1-VIII: 49–54.

Penchaszadeh, P.E. 1971b. Aspectos de la embriogénesis de algunos Gasterópodos del género *Buccinanops* D'Orbigny, 1841 (Gastropoda, Prosobranchiata, Buccinidae). Physis 30(81): 475–482.

Penchaszadeh, P.E. 1973. Nuevas observaciones sobre la reproducción de *Buccinanops gradatum* (Deshayes, 1884) (Gastropoda, Prosobranchiata, Dorsaninae). Physis 32(84): 15–18.

Portmann, A. 1925. Der einfluss der nahreier auf die larven-entwicklung von *Buccinum* und *Purpura*. Z. Morphol. Okol. Tiere 3: 526–541.

Portmann, A. 1930. Die larvennieren von *Buccinum undatum* L. Z. Zellforsch. Mikrosk. Anat. 10: 401–410.

Schafer, C.T., J.N. Smith, and R. Cote. 1990. The Saguenay Fjord: a major tributary to the Saint Lawrence Estuary, p. 378–415. *In* M. El-Sabh and N. Silverberg [ed.] Oceanography of a large scale estuarine system: the Saint Lawrence. Coastal Estuarine Stud. 39: 378–415.

SMITH, C.C., AND S.D. FRETWELL. 1974. The optimal balance between size and number of offspring. Am. Nat. 108(962): 499–506.

SPIGHT, T.M. 1976a. Hatching size and the distribution of nurse eggs among Prosobranch embryos. Biol. Bull. 150: 491–499.

SPIGHT, T.M. 1976b. Ecology of hatching size for marine snails. Oecologia 24: 283–294.

SPIGHT, T.M., C. BIRKELAND, AND A. LYONS. 1974. Life histories of large and small Murexes (Prosobranchia: Muricidae). Mar. Biol. 24: 229–242.

SPIGHT, T.M., AND J. EMLEN. 1976. Clutch sizes of two marine snails with a changing food supply. Ecology 57: 1162–1178.

STAIGER, H. 1951. Cytologische und morphologische untersuchungen zur determination der nahreier bei prosobranchiern. Z. Zellforsch. Mikrosk. Anat. 35: 496–549.

THORSON, G. 1935. Studies on the egg capsules and development of arctic marine prosobranchs. Medd. Gronl. Udgivne Kommiss. Vidensk. Undersog. I Gronl. 100(5): 1–36.

WEBBER, H.H. 1977. Gastropoda: Prosobranchia, p. 1–97. *In* A.C. Giese and J.S. Pearse [ed.] Reproduction of marine invertebrates. Vol. IV. Academic Press, New York, N.Y.

WEST, D.L. 1979. Nutritive egg determination in *Colus stimpsoni* (Prosobranchia: Buccinidae). Am. Zool. 19(523): 956.

Patterns in the Abundance and Composition of Fishes among Beds of Different Macrophytes: Viewing a Littoral Zone as a Landscape

John H. Chick[1] and Carole C. McIvor[2]

National Biological Survey, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, FL 32611-0450, USA

Chick, J.H. and C.C. McIvor. 1994. Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. Can. J. Fish. Aquat. Sci. 51: 2873–2882.

To determine if the density, biomass, species density (number of fish species per square metre), and species composition of juvenile and forage fish (fish ≤100 mm SL) differed among macrophyte types, we sampled fishes monthly from beds of *Hydrilla verticillata*, *Panicum hemitomon*, and *Potamogeton illinoensis* in two areas of Lake Okeechobee, Florida, from December 1989 to December 1990. Fish density and biomass differed significantly among the three macrophytes despite our design having relatively low statistical power to detect such differences. Densities and biomass were highest in *H. verticillata* (196 fish·m^{-2}, 30 g·m^{-2}), intermediate in *P. hemitomon* (60 fish·m^{-2}, 12 g·m^{-2}), and lowest in *P. illinoensis* (31 fish·m^{-2}, 6 g·m^{-2}). Trends among macrophytes were consistent throughout the year despite significant variation among months. Fish species density did not vary significantly among macrophyte types. However, the relative abundances of fishes differed significantly among macrophyte types. Patterns in fish abundance and relative species composition led us to infer that beds of different macrophyte types constitute distinct microhabitats for fish and structure the littoral zone of Lake Okeechobee into a mosaic landscape.

Afin de déterminer si la densité, la biomasse, la densité d'espèces (nombre d'espèces de poisson par mètre carré) et l'abondance relative des espèces de poissons juvéniles et de poissons proies (longueur standard ≤100 mm) varient en fonction des types de macrophytes présentes dans le milieu, nous avons échantillonné mensuellement les poissons dans des herbiers d'*Hydrilla verticillata*, de *Panicum hemitomon*, et de *Potamogeton illinoensis* dans deux secteurs du lac Okeechobee, en Floride, de décembre 1989 à décembre 1990. Nous avons observé des différences dans les densités et les biomasses de poissons parmi les trois types de macrophytes, bien que la puissance statistique de notre protocole était relativement faible pour la détection de ces différences. Les densités et la biomasse étaient les plus élevées dans les herbiers de *H. verticillata* (196 poissons·m^{-2}, 30 g·m^{-2}), intermédiaires dans ceux de *P. hemitomon* (60 poissons·m^{-2}, 12 g·m^{-2}) et les plus basses dans ceux de *P. illinoensis* (31 poissons·m^{-2}, 6 g·m^{-2}). Les différences observées dans les trois types d'herbiers se sont maintenues durant l'année malgré l'existence de variations intermensuelles. Selon les types de macrophytes, la densité d'espèces ne variaient pas, mais les abondances relatives des espèces variaient. Les variations dans les abondances absolues et relatives des poissons nous laissent penser que les herbiers de différents types de macrophytes forment des microhabitats distincts pour les poissons et structurent la zone riveraine du lac Okeechobee en un paysage mosaïque.

Received October 7, 1993
Accepted May 30, 1994
(J12116)

Reçu le 7 octobre 1993
Accepté le 30 mai 1994

Research on lentic populations of fishes has often focused on two major habitat types: the vegetated littoral zone and the open-water pelagic zone. It is well known that certain fishes are generally not distributed evenly throughout a lake, but are often concentrated within the vegetated littoral zone (Hall and Werner 1977; Werner et al. 1977, 1978; Gullory et al. 1979; Engel 1985; Conrow et al. 1990). Vegetated habitats tend to be populated primarily by small forage fishes and juveniles of larger species, which use these habitats as a refuge from predators and as feeding grounds (Werner et al. 1983; McIvor and Odum 1988; Rozas and Odum 1988). Although habitat partitioning between vegetated and nonvegetated habitats has been well documented (Gullory et al. 1979; Stang and Hubert 1984; Paszkowski 1985; Paller 1987; Werner and Hall 1988; Savino and Stein 1989; Gelwick and Matthews 1990; Ferrell and Bell 1991; Meals and Miranda 1991), less is known regarding fish–habitat associations within vegetated habitats at the scale of different macrophyte species or types.

Lodge et al. (1988) suggested that the patch attributes studied by landscape ecologists could usefully describe littoral habitat patches. In ecological terms, a landscape can be defined simply as a mosaic of habitat patches (Urban et al. 1987). Thus, to describe a littoral zone as a landscape, one must identify the habitat patches or landscape elements comprising the mosaic in relation to the populations or processes of interest (Forman and Godron 1986; Turner 1989). Because littoral zones often contain several macrophyte species, beds of different macrophytes are a feature that might serve as the elements comprising a littoral landscape. Beds of different

[1]Present address: Institute of Ecology, University of Georgia, Athens, GA 30602-2202, USA.
[2]Present address: National Biological Survey, Arizona Cooperative Fish & Wildlife Research Unit, University of Arizona, Tucson, AZ 85721, USA.

macrophytes can differ in water chemistry (Frodge et al. 1990) and in the abundance and composition of invertebrates (Krecker 1939; Chilton 1990; Kornijow and Gulati 1992; Lalonde and Downing 1992; Paterson 1993). Thus, one might predict that beds of different macrophytes should function as different habitats or microhabitats for fish, which, if empirically demonstrated, would confirm the relevance of this landscape definition to littoral zone fishes.

Investigations of habitat partitioning of fishes within littoral zones have focused on differences in depth or distance to shore (Hall and Werner 1977; Werner et al. 1977) and vegetation abundance (Killgore et al. 1989). Werner et al. (1977), Keast (1984), and Conrow et al. (1990) have investigated fish distribution among different macrophyte types. Of these, only Keast (1984) conducted an empirical test of fish distribution among different macrophyte types. Thus, the relevance of the landscape view suggested by Lodge et al. (1988) remains largely untested in regards to littoral zone fishes.

Lake Okeechobee, Florida, like many subtropical lakes, has an extensive littoral zone and many fishes that utilize littoral and marsh habitats either during certain life-history stages, or throughout their entire life cycle. Because of these factors, the littoral zone of Lake Okeechobee is a good site to examine whether a littoral zone is best viewed as one homogeneous habitat or as a landscape of microhabitats for fishes. Our objective for this study was to determine if the abundance and composition of juvenile and forage fish populations (fish ≤ 100 mm SL) along the western shore of Lake Okeechobee differed among macrophyte types. The main premise examined was that beds of different macrophyte types can act as microhabitats for fish and structure the littoral zone into a landscape. If this premise is true, then fish abundance and species composition should differ among macrophytes (H_a), whereas abundance and composition of fishes should not be related to macrophyte type (H_0) if the premise is false. To empirically test this hypothesis, we compared fish density (fish per square metre), biomass (grams per square metre), species density (number of species per square metre), and the relative abundance of fishes in beds of three macrophyte types.

Methods

Site Description

Lake Okeechobee is situated in the southern peninsula of Florida. Total lake area varies from 1450 to 1891 km^2, depending on water level (Brooks 1974). The majority of the 387-km^2 littoral zone in this lake is located along the western shore (Pesnell and Brown 1977, Milleson 1987). Emergent species dominate the littoral zone and include *Typha* spp., *Eleocharis cellulosa*, *Rhynchospora tracyi*, *Salix carolina*, *Panicum* spp., and other mixed grasses (Pesnell and Brown 1977, Milleson 1987). Common submersed macrophytes include *Hydrilla verticillata*, *Vallisneria americana*, *Potamogeton illinoensis*, and *Najas guadalupensis*.

We sampled beds of three macrophytes (*H. verticillata*, *Panicum hemitomon*, and *P. illinoensis*) with distinct structural characteristics. *Panicum hemitomon* is an emergent grass with a submersed structure consisting of straight round stems. *Hydrilla verticillata* is a submersed macrophyte with complex whorls of small leaves, and *Potamogeton illinoensis* is a submersed macrophyte with larger lance-shaped to oval leaves. From December 1989 to December 1990, we obtained monthly fish samples from adjacent beds of the three macrophytes in two areas. The first area is located near the Indian Prairie boat ramp (27°02′81″N, 80°56′14″W) and the second is located in Moonshine Bay (27°57′00″N, 81°03′20″W). These two areas are approximately 16.5 km apart and will be referred to as Indian Prairie and Moonshine Bay throughout this paper. Within these areas, beds of these three macrophytes often grew in close proximity to each other, which minimized the confounding effect of geographic location.

Indian Prairie is adjacent to the pelagic zone of the lake whereas Moonshine Bay is fully within the littoral zone and further from any significant pelagic region. The substrate at Indian Prairie was dominated by hard sand and shell whereas the substrate at Moonshine Bay consisted of hard sand and shell underneath a 4-cm layer of detritus or peat. Indian Prairie was exposed to more turbulence and wave action from the pelagic zone than Moonshine Bay (personal observations of the authors). During 1990, concentrations of total phosphorus, total nitrogen, and chlorophyll *a* averaged (±1 SD) 0.057 (±0.039) mg·l^{-1}, 1.57 (±0.56) mg·l^{-1}, and 13.6 (±7.8) mg·m^{-3} for Indian Prairie and 0.058 (±0.035) mg·l^{-1}, 3.11 (±1.78) mg·l^{-1}, and 19.2 (±13.2) mg·m^{-3} for Moonshine Bay (E.J. Phlipps and P.V. Zimba, Department of Fisheries and Aquaculture, University of Florida, unpublished data).

Sampling Methodology

We used two enclosure traps to sample fishes. During the first 3 mo of the study, a circular 2.27-m^2 (1.7 m diameter × 1.2 m height) drop trap based on the design of Zimmerman et al. (1983) was used. During the month of March 1990, a comparison study was conducted which showed that a square 1-m^2 throw trap would yield estimates of fish density similar to the drop trap with less effort (Chick et al. 1992). Therefore, a square 1-m^2 throw trap was used for fish sampling from April 1990 through December 1990. The construction and deployment of the 2.27-m^2 drop trap are described in Chick et al. (1992) and Chick (1992). Therefore, we will only describe the construction and methodology associated with the 1-m^2 throw trap. Both of these methods have been found to be effective for sampling fishes in shallow vegetated habitats (Kushlan 1981; Zimmerman et al. 1983; Rozas and Odum 1988; Chick et al. 1992).

The 1-m^2 throw trap was constructed from 14-gauge aluminum sheet metal and was 1 m in height. We threw the trap into the habitat, removed the vegetation within the trap, and captured fish with a 3-mm-mesh bar seine (0.99 × 1 m). We continued seining until five consecutive sweeps produced no fish. All fish captured were anesthetized with phenoxyethanol and preserved in 10% formalin for sorting and identification in the laboratory. Because of the low lake levels at the time of this study, a majority of the littoral zone could usually be sampled with this method (i.e., depths were typically <1.0 m).

Sampling Protocol

At each of the two study areas, three samples were taken from each of the three macrophyte types every month. We systematically changed the sampling order for the two study areas and the order that each macrophyte type within each area was sampled each month. All samples were taken between the hours of 07:00 and 20:00. We only sampled

H. verticillata beds where plant growth at the surface of the water formed a dense canopy or floating mat because this was the most common configuration of beds of this species. *Hydrilla verticillata* beds usually had no other co-occurring macrophyte species. *Potamogeton illinoensis* beds usually contained a majority of plants whose height reached the water surface, with subdominant *V. americana* plants (a submersed macrophyte that forms a cluster of long ribbonlike leaves) frequently co-occurring. *Panicum hemitomon* beds frequently occurred at the interface with the submersed vegetation zone of Lake Okeechobee, with understories of *P. illinoensis* or *V. americana* common. We only sampled beds of *P. illinoensis* and *P. hemitomon* where co-occurring macrophytes made up a distinct minority of the total plant growth (<20% of the visually estimated plant coverage).

Individual beds of the three macrophytes we sampled ranged in size from approximately 20 m^2 to several 100 m^2. We attempted to sample beds of each macrophyte that shared a border with at least one bed of another macrophyte type of interest (that we would also sample). Because the two study areas usually contained multiple beds of each of the macrophytes of interest, we were able to avoid sampling beds that contained visible gaps from a previous month's sampling activity. All sampling, in either Indian Prairie or Moonshine Bay, took place within an area approximately (≤)1 km^2.

In order to describe differences in physicochemical properties of the sampled macrophyte beds that might influence the habitat use by fishes, we measured surface and bottom temperature, dissolved oxygen, and conductivity within each plant bed. Water depth was measured with a pole calibrated in centimetres. Temperature and conductivity were measured with a YSI salinity–conductivity–temperature meter model 33, and a YSI oxygen meter model 58 was used to measure dissolved oxygen. From June 1990 to December 1990, we determined vegetation standing crop (wet kilograms per cubic metre) for each sample. All vegetation was placed into a plastic diving bag with a mesh bottom. After water had stopped draining from the bottom of the bag, the bag and contents were swung circularly 25 times and then weighed on a Pesola spring scale. Measurements of both water depth and vegetation height were made so that we could convert vegetation biomass (wet kilograms per square metre) to standing crop (wet kilograms per cubic metre).

Statistical Analyses

We did not use fish larger than 100 mm SL in the general analyses of this study because the 1-m^2 throw trap does not sample them adequately. Low lake levels during June 1990 prevented us from sampling the Moonshine Bay site. As a result, we have excluded the June data from all analyses. Larval fish were used in the analyses, although it is likely that the abundances of these small fish (<10 mm SL) were underestimated due to the 3-mm mesh size used on dip nets, sieves, and the bar seine. Because larvae were only captured in substantial numbers during December 1989 and January 1990, including larvae in the analyses is unlikely to have greatly affected the outcome of the statistical analyses.

We obtained three measures of juvenile and forage fish abundance: total fish density, total fish biomass, and species density (number of species per square metre). For each response variable, we calculated monthly means from the three samples taken in each macrophyte type (*H. verticillata*, *P. hemitomon*, and *P. illinoensis*) in each area. We used these means in a split-plot analysis of variance (ANOVA) testing the effects of area, macrophyte type, and month on each response variable using the following model:

$$Y = \text{Area} + \text{Macrophyte} + \text{Area·Macrophyte} + \text{Month} + \text{Month·Macrophyte} + \text{MSE}$$

where MSE is the subplot error.

The main effects of area and macrophyte were tested over the whole-plot error (area by macrophyte interaction), whereas month and the interaction of month with macrophyte were tested over MSE (GLM procedure, SAS Institute Inc. 1991). Water depth and macrophyte standing crop were analyzed separately as response variables and as covariates to fish density (i.e., as dependent variables (Y) and factors within the model). Type III sum of squares was used to calculate the mean squares for all F tests. We used least-square means to compare main effect levels when the ANOVA indicated significant main effect differences were present. To balance the probability of making type II errors with the probability of making type I errors, we established two probability (P) levels to determine significance: $P > 0.1$ were nonsignificant, $P \leq 0.1$ but > 0.05 were considered marginally significant, and $P \leq 0.05$ were significant.

We examined residual plots to determine if transformations were necessary. To conform to assumptions of normality and homoscedasticity, we used a square root transformation for density data and a logarithmic (natural log (biomass) + 1) transformation for biomass data. To examine the fish assemblages of the macrophyte types, we analyzed the densities (square root transformed) of the five most abundant species with the model above. The mean density of all species that comprised at least 1% of the total catch was also determined for each macrophyte type and area pooled across months. We ranked these means by macrophyte type and area and used a Cochran–Mantel–Haenszel (CMH) test of general association to test for differences in species rankings among macrophyte types, stratified by area (GLM procedure, SAS Institute Inc. 1991). This test can be viewed as a stratum adjusted Pearson chi-square statistic (SAS Institute Inc. 1991).

We estimated the power ($1 - \beta$) of the split-plot analyses of total fish density (square root transformed), biomass (logarithmically transformed), and species density using the "probf" function of SAS (SAS Institute Inc. 1991) and the noncentralic parameter formulas for factorial ANOVA from Winer (1971). We calculated three power estimates: one for a difference (Δ) between the largest and smallest mean = 1 SD, one for a $\Delta = 2$ SD, and one for the actual differences we observed. All power estimates were made for an α level of 0.05. The methods we used to estimate power are further described in the Appendix.

Results

Physicochemical Parameters

Beds of *H. verticillata* tended to have higher water temperature and dissolved oxygen concentration at the surface than at the bottom (Table 1). These profiles were also apparent, but to a lesser degree, in *P. illinoensis*. In *P. hemitomon*, water temperature tended to be higher near the bottom and lower at the surface whereas dissolved oxygen was higher at the surface and lower near the bottom. Water depth

TABLE 1. Mean, minimum, and maximum temperature (°C), conductivity ($\mu S \cdot cm^{-1}$), dissolved oxygen ($mg \cdot L^{-1}$), depth (cm), and vegetation standing crop (VSC, wet $kg \cdot m^{-3}$) measured in beds of three macrophyte types in Lake Okeechobee.

	H. verticillata			*P. hemitomon*			*P. illinoensis*		
Factor	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Surface temp.	26	17	35	26	14	36	26	15	35
Bottom temp.	24	16	32	27	18	36	25	9	35
Surface cond.	618	205	1000	639	330	1500	574	370	1100
Bottom cond.	602	205	1050	617	338	1500	572	190	1100
Surface O_2	14	5	>20	9	2	20	9	3	15
Bottom O_2	3	0.3	>20	5	0.5	13	5	0.4	14
Depth	63	10	90	51	10	88	68	29	98
VSC	4.9	1.7	15	3.8	0.4	12.5	1.1	0.06	5.4

TABLE 2. Results from a split-plot ANOVA testing the effects of area, macrophyte type, and month on vegetation standing crop.

Source	df	Type III sum of squares	*P*
Model	20	207.44	0.0001
Area	1	15.32	0.0762
Macrophyte	2	91.17	0.0281
Area·macrophyte[a]	2	2.63	0.3897
Month	5	38.34	0.0034
Month·macrophyte	10	59.98	0.0042
Error	15	19.66	
Corrected total	35	227.10	

[a]Whole-plot error — used for testing the area and macrophyte main effects.

did not differ significantly among areas ($P = 0.88$) or macrophyte types ($P = 0.53$). Water depth did change significantly ($P = 0.0001$) among months.

Vegetation standing crop (wet kilograms per cubic metre) differed significantly among macrophyte types (Table 2). *Hydrilla verticillata* had significantly higher standing crops than both *P. hemitomon* and *P. illinoensis*, and standing crops of *P. hemitomon* were marginally higher than of *P. illinoensis*. Differences between areas were marginally significant, as standing crop tended to be higher in Moonshine Bay than in Indian Prairie. This analysis also showed that the differences in vegetation standing crop among months were significant and that the differences among macrophytes interacted significantly with month. Whereas the standing crop of *H. verticillata* was consistently higher than of *P. illinoensis* and *P. hemitomon*, the magnitude of these differences was not consistent among months.

Catch Synopsis

A total of 27 103 juvenile and forage fish were captured including 26 species and nine families (Table 3). Individuals from the families Poeciliidae and Cyprinodontidae dominated the collections, accounting for 96% of the numerical catch and 76% of the biomass. The five most abundant species (numerically and by weight) were *Heterandria formosa, Gambusia holbrooki, Poecilia latipinna, Lucania goodei,* and *Jordanella floridae*. Centrarchids made up a small percentage (3%) of the total catch in terms of numbers, but made up a considerable amount (21%) of the total fish biomass collected. Two species of gobies, *Gobiosoma bosc* and *Microgobius gulosus*, were captured only in the Indian Prairie area. These species are generally associated with marine or estuarine environments.

Fish Density, Biomass, and Species Density

Fish density and biomass differed significantly among macrophyte types and months (Table 4). Species density differed significantly among months, but was not significantly related to macrophyte type (Table 4). When added to the model as covariates, neither depth nor vegetation standing crop was related to fish density ($P = 0.26$ and 0.42, respectively) and fish density still differed significantly ($P = 0.0292$) among macrophyte types. However, with these covariates added to the model, variation in fish density among months was no longer significant ($P = 0.7078$). This suggests that some of the monthly variation in fish density can be explained by (or was affected by) concurrent changes in depth and vegetation standing crop.

Least-square means revealed that fish density and biomass were significantly higher ($P \leq 0.05$) in *H. verticillata* than in *P. hemitomon* and *P. illinoensis* (Fig. 1a and 1b). This trend was consistent throughout the year, even though fish abundance rose substantially in late spring and early summer (Fig. 1a and 1b). Differences between *P. hemitomon* and *P. illinoensis* were not significantly different ($P > 0.1$). Although not statistically significant, species density tended to be highest in *H. verticillata* and lowest in *P. illinoensis* (Fig. 1c).

For all three response variables, our experimental design had relatively high power to test for significance of the interaction between area and macrophyte type and for both the area and month main effects. Our design had relatively low power to test for significance of the interaction between month and macrophyte type and for the macrophyte type main effect. There was no significant difference in fish density,

TABLE 3. Total number of juvenile and forage fishes captured from December 1989 to December 1990 in *H. verticillata*, *P. hemitomon*, and *P. illinoensis* beds from the two study areas along the western shore of Lake Okeechobee.

Species	*H. verticillata*	*P. hemitomon*	*P. illinoensis*		% of total catch (all habitats)
Poeciliidae					
Heterandria formosa	6 381	1183	509		30
Gambusia holbrooki	3 830	2221	700		25
Poecilia latipinna	3 370	759	332		17
Cyprinodontidae					
Lucania goodei	2 972	967	701		17
Jordanella floridae	1 359	138	209		6
Fundulus chrysotus	144	120	28		1
Fundulus seminolis	34	23	38		<1
Cyprinodon variegatus	4	2	36		<1
Fundulus confluentus	0	2	0		<1
Centrarchidae					
Lepomis macrochirus	158	28	119		1
Lepomis microlophus	30	92	64		1
Enneacanthus gloriosus	167	9	9		1
Lepomis marginatus	16	26	52		<1
Lepomis punctatus	8	14	15		<1
Lepomis gulosus	28	1	0		<1
Micropterus salmoides	2	3	3		<1
Gobiidae					
Microgobius gulosus	4	8	69		<1
Gobiosoma bosc	0	4	13		<1
Percidae					
Etheostoma fusiforme	9	19	23		<1
Cyprinidae					
Notemigonus crysoleucas	1	20	3		< 1
Notropis maculatus	1	1	2		<1
Ictaluridae					
Ictalurus natalis	7	0	0		<1
Noturus gyrinus	0	1	0		<1
Atherinidae					
Menidia beryllina	1	3	2		<1
Catostomidae					
Erimyzon sucetta	1	2	0		<1
Cichlidae					
Tilapia aurea	0	1	2		<1
Total	18 527	5647	2929	=	27 103

biomass, or species density among the study areas, and the area by macrophyte type interaction was not significant for any of these three response variables (Table 4). Had differences approached 2 SD of the grand mean, our design would have had high power to test for the significance of these factors (Table 4). The month by macrophyte interaction was not significant for any of the three response variables, but we had little power to test for the significance of this interaction (Table 4). Our data do not suggest an important month by macrophyte type interaction for either fish density or biomass (Fig. 1a and 1b). Species density data was highly variable and little can be concluded from our test of the month by macrophyte type interaction or the macrophyte type main effect on species density, since our power to test for the significance of these effects was low (Table 4; Fig. 1c).

Fish Assemblages

Nine species were captured frequently enough for their individual catch to comprise at least 1% of the total. The rankings of these nine species differed significantly among macrophyte types (CMH, $P = 0.001$). Species rankings within *H. verticillata* appeared to be different from *P. hemitomon* and *P. illinoensis* whereas differences between *P. hemitomon* and *P. illinoensis* are less clear (Fig. 2). *H. formosa* and *P. latipinna* tended to be the two most abundant species in *H. verticillata* whereas *G. holbrooki* and *L. goodei* tended to be the most abundant species in *P. hemitomon* and *P. illinoensis*. Of the 17 species that comprised less than 1% of the total catch, 16 were captured in *P. hemitomon*, 13 in *H. verticillata*, and 12 in *P. illinoensis* (Table 3).

For the five most abundant species captured in this study, there was a consistent trend of *H. verticillata* containing the highest mean densities followed by *P. hemitomon* and *P. illinoensis* (Fig. 3). The densities of *H. formosa*, *P. latipinna*, and *J. floridae* were significantly related to macrophyte type, and the densities of *G. holbrooki* were marginally related to macrophyte type (Table 5). Mean densities of *L. goodei* over the year were highest in *H. verticillata* followed by *P. hemitomon* and *P. illinoensis* (Fig. 3). However, significant interactions with area and marginally significant interactions with month clouded this statistical relation (Table 5; Fig. 4a and 4b). Differences in the densities of

TABLE 4. Results from the split-plot ANOVA testing the effects of area, macrophyte type, and month on fish density, biomass, and species density.

Source	df	SS type III	*P*	Power[a] Δ = 1 SD	Power Δ = 2 SD	Power Δ observed
Fish density: $\mu = 68\ fish \cdot m^{-2}$, $SD = 19 \cdot m^{-2}$						
Model	38	4356.08	0.0001			
Area	1	150.15	0.1364	0.50	0.93	0.13
Macrophyte	2	2588.76	0.0194	0.24	0.61	0.61
Area·macrophyte[b]	2	51.19	0.2806	0.84	0.99	0.12
Month	11	896.42	0.0008	0.28	0.91	0.71
Month·macrophyte	22	352.41	0.6724	0.13	0.50	0.16
Error	31	599.14				
Fish biomass: $\mu = 9.8\ g \cdot m^{-2}$, $SD = 3.3\ g \cdot m^{-2}$						
Model	38	193.67	0.0002			
Area	1	4.44	0.2669	0.49	0.92	0.09
Macrophyte	2	98.94	0.0372	0.23	0.59	0.43
Area·macrophyte[b]	2	3.82	0.2672	0.84	0.99	0.15
Month	11	50.27	0.0044	0.29	0.91	0.58
Month·macrophyte	22	21.44	0.8033	0.13	0.50	0.14
Error	31	43.01				
Species density: $\mu = 5.04\ species \cdot m^{-2}$, $SD = 2.59\ species \cdot m^{-2}$						
Model	38	565.01	0.0130			
Area	1	60.62	0.1400	0.44	0.89	0.14
Macrophyte	2	167.8	0.1129	0.21	0.54	0.17
Area·macrophyte[b]	2	21.35	0.2214	0.84	0.99	0.13
Month	11	154.88	0.0528	0.28	0.91	0.35
Month·macrophyte	22	130.55	0.6167	0.13	0.49	0.16
Error	31	208.99				

[a]Power = $1-\beta$; Δ = the difference between the largest and smallest means.
[b]Whole-plot error — used for testing the area and macrophyte main effects.

P. latipinna among months were significant, as was the interaction between macrophyte type and month (Table 5; Fig. 4c). During the first 3 mo of this study, *P. latipinna* densities were low in all three macrophyte types. Thereafter, densities of *P. latipinna* rose dramatically, especially in *H. verticillata*.

Discussion

Viewing a Littoral Zone as a Landscape

Our observed differences in the abundance and composition of fishes among macrophyte types in Lake Okeechobee are consistent with other studies which have found nonhomogeneous fish distributions within the littoral zones of other lakes (Werner et al. 1977; Keast 1984; Conrow et al. 1990). Our results support the hypothesis that beds of different macrophyte types comprise distinct microhabitats for juvenile and forage fish. From the perspective of these fishes, the Lake Okeechobee littoral zone may be better described as a landscape of microhabitats, with beds of different macrophyte types as the microhabitat patches or elements comprising this mosaic, than as one homogeneous habitat (Forman and Godron 1986).

Lodge et al. (1988) suggested that many of the concepts of landscape ecology might be successfully tested within littoral zones, although landscape ecology has traditionally focused on larger scale (i.e., square kilometres) habitat mosaics than most littoral zones. The results of our study are consistent with Lodge et al. (1988)'s notion of a littoral landscape. Wiens and colleagues (Wiens 1989, 1992; Wiens and Milne 1989; Crist et al. 1992) have advanced a "multiscale perspective on landscape patterns and dynamics" that suggests that the concepts of landscape ecology apply to any scale. For example, populations of epibiont organisms that live on the surface of zooplankton can be viewed as existing in a landscape consisting of individual zooplanktors as habitat patches (or landscape elements) in a matrix of water (Threlkeld et al. 1993). From an ecological standpoint, a landscape may be more important as a "criterion for observations" than as a physical entity (Allen and Hoekstra 1992). Thus, when we describe the littoral zone of Lake Okeechobee as a landscape, we are describing a way of observing and studying the littoral zone and the fishes inhabiting it.

In the present study, fish abundance was related to macrophyte type, but not to vegetation standing crop or water depth. The lack of a statistical relation between vegetation standing crop and fish density is surprising because patterns of vegetation standing crop among macrophytes were similar to patterns of fish abundance (i.e., highest in *H. verticillata* and lowest in *P. illinoensis*). Other studies have found, or hypothesized, a relation between fish abundance and vegetation abundance (Cooper and Crowder 1979; Wiley et al. 1984; Moxley and Langford 1985; Killgore et al. 1989). Variation in standing crop among months may have obscured the relation between vegetation standing crop and fish density. Additionally, habitat characteristics of these different

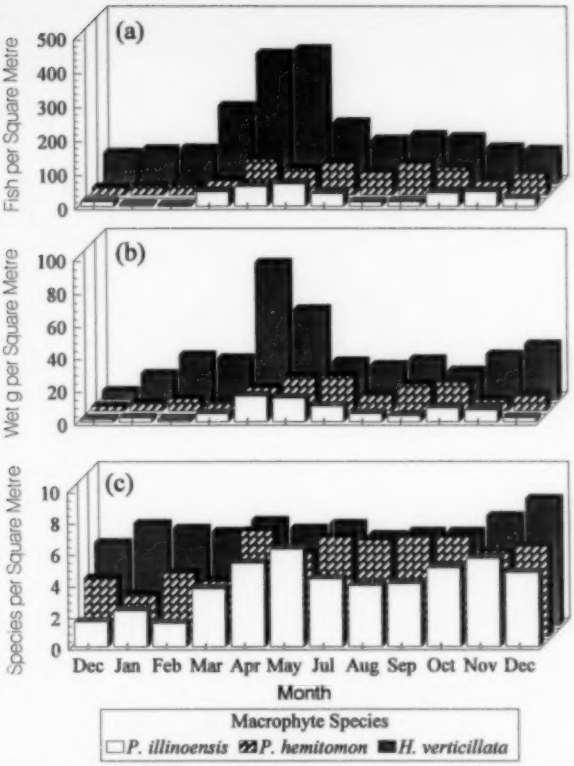


FIG. 1. (a) Mean juvenile and forage fish density, (b) biomass, and (c) species density in beds of *H. verticillata*, *P. hemitomon*, and *P. illinoensis* by month.

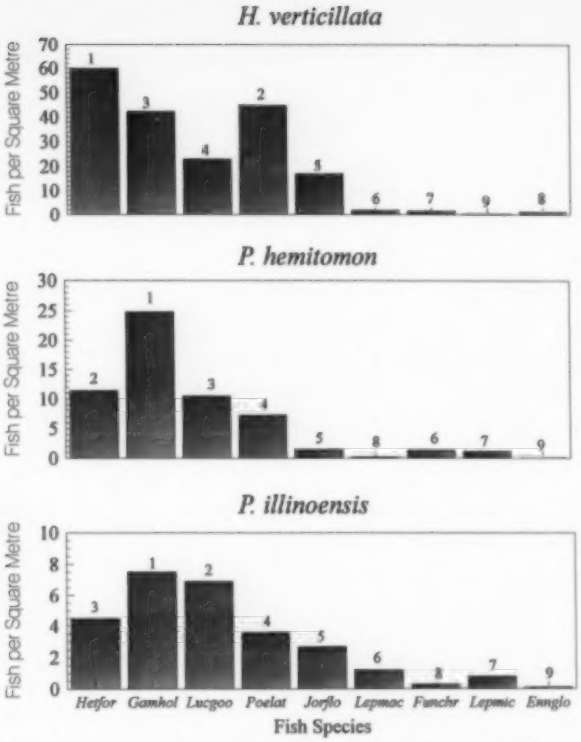


FIG. 2. Mean densities of the nine most abundant juvenile and forage fish species captured by macrophyte type. Numbers above bars are the species rankings within each macrophyte type. Fish species: Hetfor = *Heterandria formosa*, Gamhol = *Gambusia holbrooki*, Lucgoo = *Lucania goodei*, Poelat = *Poecilia latipinna*, Jorflo = *Jordanella floridae*, Lepmac = *Lepomis macrochirus*, Funchr = *Fundulus chrysotus*, Lepmic = *Lepomis microlophus*, Ennglo = *Enneacanthus gloriosus*.

macrophyte types other than vegetation standing crop may have influenced fish abundance and composition.

Lillie and Budd (1992) hypothesized that habitat architecture would affect the habitat quality of macrophytes for fish and invertebrates. In our study, several architectural parameters varied among the macrophyte types studied. Vegetation abundance (or standing crop) differed among the three macrophytes sampled causing heterogeneity on a horizontal plane. On a vertical plane, each of the macrophytes uniquely apportioned their biomass through the water column (i.e., the extent of canopy formation). The three macrophytes also differed in regard to the amount of branching and the size, amount, and position of leaves. *Hydrilla verticillata* plants tended to have the most extensive branching and densest canopies of the three macrophytes (personal observation of the authors). Differences in canopy formation probably influenced the characteristic temperature and oxygen clines found among the three macrophytes and other water quality parameters (Frodge et al. 1990). These differences may have caused habitat quality differences among the three macrophytes that affected the habitat use of the fish.

Possible Mechanisms Explaining Differences in Fish Distribution

Explanations for the distribution of juvenile and forage fish between littoral and other habitats have centered around differences in food resources and refuge from predators. It is likely that both predation pressure and food availability influenced the distributions of fish in this study. For example, juvenile and forage fishes feed on a variety of invertebrates, and the distributions of invertebrates are known to differ with macrophyte type (Krecker 1939; Chilton 1990; Hargeby 1990). Additionally, differences in plant surface area and vegetation decomposition could impact epiphytic communities and detrital food webs associated with these macrophytes (Paterson 1993). Predation pressure probably also differs among macrophyte types because differences in vegetation density can greatly affect the ability of predators to capture prey (Savino and Stein 1982). Macrophyte growth forms can affect both the ability of predators to capture small fish and the ability of these small fish to capture invertebrate prey (Ryer 1988; Dionne and Folt 1991; Lillie and Budd 1992).

A number of mechanisms might be responsible for the fish distributions found in this study. First, if fish movement among macrophyte beds is negligible or random, differences in fish survival could have resulted from differences in prey availability and mortality from predators among the three macrophytes. Second, because many fishes are mobile and selective in regards to habitat use, it seems plausible that the distributions found were influenced by

TABLE 5. *P* values associated with split-plot ANOVA testing the effects of area, macrophyte type, and month on the densities of *H. formosa*, *G. holbrooki*, *P. latipinna*, *L. goodei*, and *J. floridae*.

Source	*P* *H. formosa*	*P* *G. holbrooki*	*P* *P. latipinna*	*P* *L. goodei*	*P* *J. floridae*
Model	0.0001	0.0311	0.0001	0.0051	0.0005
Area	0.0531	0.3294	0.1632	0.3224	0.0276
Macrophyte	0.0303	0.0720	0.0267	0.3224	0.0172
Area·macrophyte[a]	0.1194	0.2497	0.4049	0.0148	0.6982
Month	0.0001	0.1682	0.0004	0.3912	0.0041
Month·macrophyte	0.1551	0.9326	0.0339	0.0643	0.4299

[a]Whole-plot error — used for testing the area and macrophyte main effects.

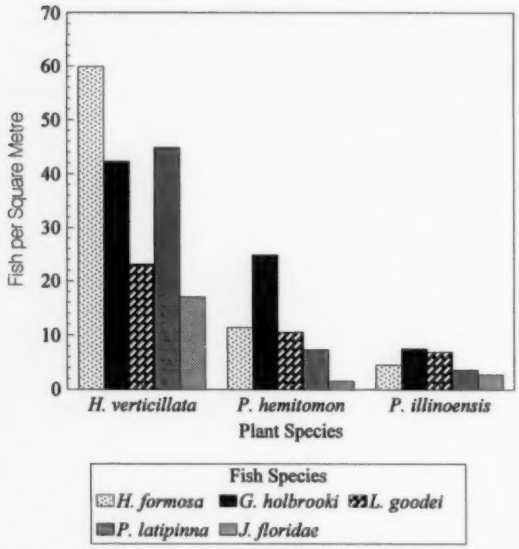


FIG. 3. Mean densities of the five most abundant juvenile and forage fish species captured in this study by macrophyte type. The five most abundant species were *H. formosa*, *G. holbrooki*, *L. goodei*, *P. latipinna*, and *J. floridae*.

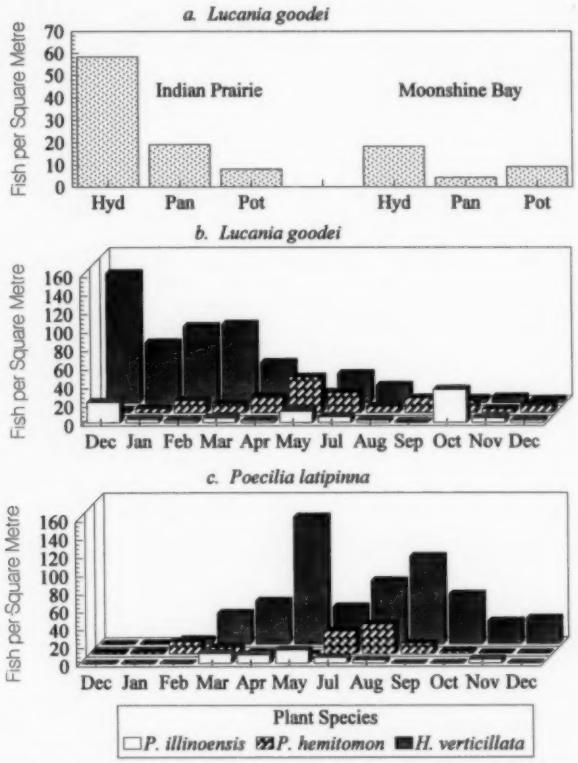


FIG. 4. Graphical illustration of significant interactions in the fish density data between (a) macrophyte type and area for *L. goodei* (Hyd = *H. verticillata*, Pan = *P. hemitomon*, Pot = *P. illinoensis*), (b) macrophyte type and month for *L. goodei*, and (c) macrophyte type and month for *P. latipinna*.

movement and active selection among macrophyte types. Bell and Westoby (1986) and Gotceitas and Colgan (1987, 1990) have conducted laboratory and manipulative field studies that indicate that fish select among vegetative microhabitats based on both prey resources and refuge from predators. In laboratory experiments we have conducted, fish actively selected among areas containing different macrophytes (the same as sampled in this study) in response to a predator (Chick 1992).

A third factor that could have influenced the distributions of juvenile and forage fishes observed in Lake Okeechobee is the selection of spawning sites. If adults were to choose differentially among macrophyte types as spawning substrate and larvae did not disperse from these spawning areas, differences in abundance of juvenile fish might occur as a result. More research is needed to determine which of these mechanisms are valid because a mensurative study such as ours can not determine the cause of the observed fish distributional patterns.

Finally, the possibility remains that larvae settle randomly among macrophyte types and the distribution patterns we found were simply coincidental. This explanation is unlikely because distribution patterns among macrophytes were similar in the two study areas and were consistent year-round despite large fluctuations in overall fish abundance.

Experimental Design and Power

Fish density and biomass were significantly related to macrophyte type even though our experimental design had relatively little power (i.e., ≤0.61) to test for these differences. Adding more areas to our design would have increased our power substantially. The extent or size of blocks and the arrangement of the sampled habitats within a block are also important in the design of distributional studies. Island

biogeography and landscape ecology theory suggest that the abundance and composition of fishes within a macrophyte bed will be affected by surrounding habitat patches (MacArthur and Wilson 1967; Pulliam 1988; Pulliam et al. 1992). Had we not sampled adjacent beds of different macrophyte types, variation in the habitats surrounding each macrophyte bed could have obscured our findings. Similar work in other lakes will be needed to determine the generality of our findings. We suggest that the blocking scheme used, in terms of the number of blocks, the size of blocks, and the proximity of the habitats of interest within a block, is important to consider in the design and interpretation of distributional studies.

Summary

We found significant differences in the density, biomass, and relative abundances of juvenile and forage fishes among three macrophyte types in Lake Okeechobee, Florida. Our results support the hypothesis that beds of different macrophyte types can function as different microhabitats for fish. We suggest that as habitat for small fishes, the littoral zone of Lake Okeechobee can be viewed as a landscape comprising the microhabitats formed by beds of different macrophyte types. We believe that a landscape view of littoral zones will prove useful for applied lake management, such as habitat manipulation and littoral zone restructuring (Engel 1987), as well as for ecological investigations on fish population dynamics and lake processes.

Acknowledgements

We thank Paul Ritter, Frank Jordan, Kristina Jackson, and Eric Flickenger for field and laboratory assistance. This research was completed in partial fulfillment of the requirements for a M.S. degree in the Department of Fisheries and Aquaculture at the University of Florida. We thank Dan Canfield, Chuck Cichra, and Wiley Kitchens for their contributions towards this work as part of Mr. Chick's graduate committee. Frank Jordan, Gary Grossman, Ron Pulliam, Karen Porter, Scott Hinch, and an anonymous reviewer provided helpful comments on this manuscript. Steve Linda, Dave Smith, and Mike Conroy provided invaluable assistance with our statistical analyses. Funding for this research was provided by the South Florida Water Management District. Logistical support was provided by the Florida Cooperative Fish and Wildlife Research Unit, the Department of Fisheries and Aquaculture at the University of Florida, U.S. Fish and Wildlife Service National Fisheries Research Center, Gainesville, Fla., and the Georgia Cooperative Fish and Wildlife Research Unit.

References

ALLEN, T.F.H., AND T.W. HOEKSTRA. 1992. Toward a unified ecology. Complexity in ecological systems series. Columbia University Press, New York, N.Y. 384 p.

BELL, J.D., AND M. WESTOBY. 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. Oecologia 68: 205–209.

BROOKS, H.K. 1974. Lake Okeechobee, p. 256–286 *In* P.J. Gleason [ed.] Environments of South Florida: past and present. Memoir 2 — Miami Geological Society. Miami, Fla.

CHICK, J.H. 1992. Aquatic macrophyte types as individual microhabitats: the distribution of juvenile and forage fishes in selected littoral habitats of Lake Okeechobee. M.S. thesis, University of Florida, Gainesville, Fla. 109 p.

CHICK, J.H., F. JORDAN, J.P. SMITH, AND C.C. MCIVOR. 1992. A comparison of four enclosure traps and methods used to sample fishes in aquatic macrophytes. J. Freshwater Ecol. 7: 353–361.

CHILTON, E.W. 1990. Macroinvertebrate communities associated with three aquatic macrophytes (*Ceratophyllum demersum*, *Myriophyllum spicatum*, and *Vallisneria americana*) in Lake Onalaska, Wisconsin. J. Freshwater Ecol. 5: 455–466.

CONROW, R., A.V. ZALE, AND R.W. GREGORY. 1990. Distributions and abundances of early life stages of fishes in a Florida lake dominated by aquatic macrophytes. Trans. Am. Fish. Soc. 119: 521–528.

COOPER, W.E., AND L.B. CROWDER. 1979. Patterns of predation in simple and complex environments, p. 257–267. *In* R.H. Stroud and H. Clepper [ed.] Predator–prey systems in fisheries management. Sport Fishing Institute, Washington, D.C.

CRIST, T.O., D.S. GUERTIN, J.A. WIENS, AND B.T. MILNE. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. Funct. Ecol. 6: 546–554.

DIONNE, M., AND C.L. FOLT. 1991. An experimental analysis of macrophyte growth forms as fish foraging habitat. Can. J. Fish. Aquat. Sci. 48: 123–131.

ENGEL, S. 1985. Aquatic community interactions of submersed macrophytes. Tech. Bull. No. 156. Department of Natural Resources, Madison, Wis. 70 p.

ENGEL, S. 1987. The restructuring of littoral zones. Lake Reservoir Manage. 3: 235–242.

FERRELL, D., AND J.D. BELL. 1991. Differences among assemblages of fish associated with *Zostera capricorni* and bare sand over a large spatial scale. Mar. Ecol. Prog. Ser. 72: 15–24.

FORMAN, R.T.T., AND M. GODRON. 1986. Landscape ecology. John Wiley & Sons, New York, N.Y. 619 p.

FRODGE, J.D., A.L. THOMAS, AND G.B. PAULEY. 1990. Effects of canopy formation by floating and submerged aquatic macrophytes on the water quality of two shallow Pacific Northwest lakes. Aquat. Bot. 38: 231–248.

GELWICK, F.P., AND W.J. MATTHEWS. 1990. Temporal and spatial patterns in littoral-zone fish assemblages of a reservoir (Lake Texoma, Oklahoma–Texas, U.S.A.). Environ. Biol. Fishes 27: 107–120.

GOTCEITAS, V., AND P. COLGAN. 1987. Selection between densities of artificial vegetation by young bluegill sunfish avoiding predation. Trans. Am. Fish. Soc. 116: 40–49.

GOTCEITAS, V., AND P. COLGAN. 1990. The effects of prey availability and predation risk on habitat selection by juvenile bluegill sunfish. Copeia 2: 409–417.

GULLORY, V., M.D. JONES, AND M. REBEL. 1979. A comparison of fish communities in vegetated and beach habitats. Q. J. Fla. Acad. Sci. 42: 113–122.

HALL, D.J., AND E.E. WERNER. 1977. Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. Trans. Am. Fish. Soc. 106: 545–555.

HARGEBY, A. 1990. Macrophyte associated invertebrates and the effect of habitat permanence. Oikos 57: 338–346.

KEAST, A. 1984. The introduced aquatic macrophyte, *Myriophyllum spicatum*, as habitat for fish and their invertebrate prey. Can. J. Zool. 62: 1289–1303.

KILLGORE, K.J., R.P. MORGAN II, AND N.B. RYBICKI. 1989. Distribution and abundance of fishes associated with submersed aquatic plants in the Potomac River. N. Am. J. Fish. Manage. 9: 101–111.

KORNIJOW, R., AND R.D. GULATI. 1992. Macrofauna and its ecology in Lake Zwemlust, after biomanipulation. II. Fauna inhabiting hydrophytes. Arch. Hydrobiol. 123: 349–359.

KRECKER F. 1939. A comparative study of the animal population of certain submersed aquatic plants. Ecology 20: 553–562.

KUSHLAN, J.A. 1981. Sampling characteristics of enclosure fish traps. Trans. Am. Fish. Soc. 110: 557–562.

LALONDE, S., AND J.A. DOWNING. 1992. Phytofauna of eleven macrophyte beds of differing trophic status, depth, and composition. Can. J. Fish. Aquat. Sci. 49: 992–1000.

LILLIE, R.A., AND J. BUDD. 1992. Habitat architecture of *Myriophyllum spicatum* L. as an index to habitat quality for fish and macroinvertebrates. J. Freshwater Ecol. 7: 113–125.

LODGE, D.M., J.W. BARKO, D. STRAYER, J.M. MELACK, G.G. MITTELBACH, R.W. HOWARTH, B. MENGE, AND J.E. TITUS. 1988. Spatial heterogeneity and habitat interactions in lake communities, p. 181–208 *In* S.R. Carpenter [ed.] Complex interactions in lake communities. Springer-Verlag, New York, N.Y.

MACARTHUR, R.H., AND E.O. WILSON. 1967. The theory of island biogeography. Princton University Press, Princeton, N.J. 203 p.

MCIVOR, C.C., AND W.E. ODUM. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. Ecology 69: 1341–1351.

MEALS, K.O., AND L.E. MIRANDA. 1991. Variability in abundance of age-0

centrarchids among littoral habitats of flood control reservoirs in mississippi. N. Am. J. Fish. Manage. 11: 298–304.
MILLESON, J.F. 1987. Vegetation changes in the Lake Okeechobee littoral zone: 1972 to 1982. Tech. Publ. No. 87-3. South Florida Water Management District, West Palm Beach, Fla. 33 p.
MOXLEY, D.J., AND F.H. LANGFORD. 1985. Beneficial effects of hydrilla on two eutrophic lakes in central Florida. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 39: 1–16.
PALLER, M.H. 1987. Distribution of larval fish between macrophyte beds and open channels in a southeastern floodplain swamp. J. Freshwater Ecol. 4: 191–200.
PASZKOWSKI, C.A. 1985. The foraging behavior of the central mudminnow and yellow perch: the influence of foraging site, intraspecific and interspecific competition. Oecologia 66: 271–279.
PATERSON, M. 1993. The distribution of microcrustacea in the littoral zone of a freshwater lake. Hydrobiologia 263: 173–183.
PESNELL, G.L., AND R.T. BROWN III. 1977. The major plant communities of Lake Okeechobee, Florida, and their associated inundation characteristics as determined by gradient analysis. Tech. Publ. No. 77-1. South Florida Water Management District, West Palm Beach, Fla. 68 p.
PULLIAM, R.H. 1988. Sources, sinks and population regulation. Am. Nat. 132: 652–661.
PULLIAM, R.H., J.B. DUNNING, JR., AND J. LIU. 1992. Population dynamics in complex landscapes: a case study. Ecol. Appl. 2: 165–177.
ROZAS, L.P., AND W.E. ODUM. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77: 101–106.
RYER, C.H. 1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. Mar. Ecol. Prog. Ser. 48: 37–45.
SAS INSTITUTE INC. 1991. SAS/STAT™ user's guide, Release 6.04 edition. SAS Institute Inc., Cary, NC. 1028 p.
SAVINO, J.F., AND R.A. STEIN. 1982. Predator–prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Trans. Am. Fish. Soc. 111: 255–266.
SAVINO, J.F., AND R.A. STEIN. 1989. Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. Environ. Biol. Fishes 24: 287–293.
STANG, D.L., AND W.A. HUBERT. 1984. Spatial separation of fishes captured in passive gear in a turbid prairie lake. Environ. Biol. Fishes 2: 309–314.
THRELKELD, S.T., D.A. CHIAVELLI, AND R.L. WILLEY. 1993. The organization of zooplankton epibiont communities. Trends Ecol. Evol. 6: 317–321.
TURNER, M.G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. 20: 171–197.
URBAN, D.L., R.V. O'NEILL, AND H.H. SHUGART, JR. 1987. Landscape ecology: a hierarchical perspecitve can help scientists understand spatial patterns. BioScience 37: 119–127.
WERNER, E.E., J.F. GILLIAM, D.J. HALL, AND G.G. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540–1548.
WERNER, E.E., AND D.J. HALL. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate – predation risk trade-off. Ecology 69: 1352–1366.
WERNER, E.E., D.J. HALL, D.R. LAUGHLIN, D.J. WAGNER, L.A. WILSMANN, AND F.C. FUNK. 1977. Habitat partitioning in a freshwater fish community. J. Fish. Res. Board Can. 34: 360–370.
WERNER, E.E., D.J. HALL, AND M.D. WERNER. 1978. Littoral zone fish communities of two Florida lakes and a comparison with Michigan lakes. Environ. Biol. Fishes 3: 163–172.
WIENS, J.A. 1989. Spatial scaling in ecology. Funct. Ecol. 3: 385–397.
WIENS, J.A. 1992. What is landscape ecology, really? Landscape Ecol. 7: 149–150.
WIENS, J.A., AND B.T. MILNE. 1989. Scaling of "landscapes" in landscape ecology, or, landscape from a beetle's perspective. Landscape Ecol. 3: 87–96.
WILEY, M.J., R.W. GORDEN, S.W. WAITE, AND T. POWLESS. 1984. The relationship between aquatic macrophytes and sportfish production in Illinois ponds: a simple model. N. Am. J. Fish. Manage. 4: 111–119.
WINER, B.J. 1971. Statistical principles in experimental design. McGraw-Hill Company, New York, N.Y. 907 p.
ZIMMERMAN, R.J., T.J. MINELLO, AND G. ZAMORA, JR. 1983. Selection of vegetated habitat by brown shrimp, *Penaeus atecus*, in a Galveston Bay salt marsh. Fish. Bull. 62: 325–336.

Appendix

The "probf" function of SAS can be used to estimate β for an F test based on the chosen α level, the degrees of freedom in the numerator, the degrees of freedom in the denominator, and the noncentralic parameter (SAS Institute Inc.). We used the following formulae to calculate the noncentralic parameter (nc):
For main effects:

$$\text{nc} = \frac{N\Sigma\tau_i^2}{\sigma}$$

$$\tau_i = \bar{y}_i - \mu$$

where μ = the grand mean of the data, $\bar{y}_i$ = the mean of factor y at level i, N = the number of observations at each level of y, and σ = the error term used in the F test (whole-plot error or split-plot error).
For interactions:

$$\text{nc} = \frac{N\Sigma\tau_{ij}^2}{\sigma}$$

$$\tau_{ij} = \bar{y}_{ij} - \bar{y}_{.j} - \bar{y}_{i.} + \mu$$

where μ = the grand mean of the data, $\bar{y}_{ij}$ = the mean of the interaction at levels i of factor I and j of factor J, $\bar{y}_{.j}$ = the mean at level j of factor J over all levels of I, $\bar{y}_{i.}$ = the mean at level i of factor I over all levels of J, N = the number of observations at each level of the interaction, and σ = the error term used in the F test (whole-plot error, or split-plot error).

In addition to determining power using the actual data, we also conducted two power analyses where we specified the Δ between the largest and smallest means in terms of standard deviations from the overall mean. For main effects with more than two levels (macrophyte type and month), we assumed a linear distribution between the largest and the smallest means. For the interaction between area and macrophyte type, we assumed a linear distribution among macrophyte types where the distribution in one area was the opposite of the distribution in the second area. For the interaction between month and macrophyte type, we assumed that one macrophyte type did not vary among months whereas the other two macrophyte types varied linearly but oppositely among months.

ANNOUNCEMENTS / AVIS

15th International Symposium of the North American Lake Management Society (NALMS)

November 6–11, 1995
Toronto, Ontario

The 15th International Symposium of NALMS will be held in Toronto, Ontario, Canada, at the Westin Harbour Castle, November 6–11, 1995. Our theme is *Aquatic Ecosystem Stewardship*. The purpose of NALMS is "to forge partnerships among citizens, scientists, and professionals to foster the management and protection of lakes and reservoirs for today and tomorrow". The Federation of Ontario Cottagers Association (FOCA) has agreed to join us in Toronto for their annual autumn meeting. FOCA has an active environment committee and a strong Lake Steward programme. Special sessions include recovery of damaged ecosystems, lake management north of 60, preimpoundment planning of reservoir management, fish stocking as a management tool, rehabilitation and management of urban lakes and reservoirs, anoxia and phosphorus, and wetland restoration. For further information, contact Dr. Frances Pick (telephone: 613-744-4254; e-mail: frpick@acadvm1.uottawa.ca) or Dr. Neil Hutchinson (telephone: 705-766-2418; facsimile: 705-766-2254).

15e symposium international de la North American Lake Management Society (NALMS)

du 6 au 11 novembre 1995
Toronto (Ontario)

Le 15e symposium international de la NALMS aura lieu à Toronto (Ontario), Canada (au Westin Harbour Castle), du 6 au 11 novembre 1995. Le thème choisi est *La gestion des écosystèmes aquatiques*. Le but de la NALMS est de « créer des partenariats entre les citoyens, les scientifiques et les professionnels pour encourager l'aménagement et la protection des lacs et des réservoirs pour le présent et l'avenir ». La fédération ontarienne des propriétaires de chalets (FOCA) a décidé de se joindre à nous à Toronto pour tenir leur réunion annuelle de l'automne. FOCA comprend un comité environnemental très actif et un programme de Gérants des Lacs. Quelques sessions planifiées sont la réhabilitation des écosystèmes endommagés, l'aménagement des lacs au nord du 60e parallèle, la planification des réservoirs avant inondation, la restauration et l'aménagement des lacs urbains, l'ensemencement des lacs comme outil de gestion, l'anoxie et le phosphore et la restauration des marécages lacustres. Pour de plus amples renseignements, communiquez avec Frances Pick (téléphone : 613-744-4254; courrier électronique : frpick@acadvm1.uottawa.ca) ou Neil Hutchinson (téléphone : 705-766-2418; télécopieur : 705-766-2254).

SYMPOSIUM 1995 QUÉBEC

FAO 1945 • 1995

LE SYMPOSIUM INTERNATIONAL DE LA FAO

Les gouvernements du Canada et du Québec et la Ville de Québec sont heureux de vous inviter au Symposium International du 50e anniversaire de l'organisation des Nations Unies pour l'alimentation et l'agriculture (FAO) à Québec, Canada. Il portera le thème **"L'humain au coeur du développement : la sécurité alimentaire par son savoir-faire".**

11-13 octobre 1995

L'esprit du Symposium

- Mettre l'accent sur la sécurité alimentaire des peuples.
- Privilégier le savoir-faire comme piste principale dans la recherche de solutions.
- Inviter des personnalités politiques et des acteurs «terrain» (entreprises et ONG) déterminés à s'engager dans la recherche de solutions originales.

Trois sous-thèmes

- La gestion des ressources naturelles.
- La gestion des marchés.
- La gestion des savoirs et de la technologie.

Information ou inscription
Monsieur Jean Lamontagne
Symposium FAO 1995
65, rue Sainte-Anne, bureau 100
Québec (Québec)
Tél.: (418) 691-7849
Fax : (418) 691-7815

THE FAO INTERNATIONAL SYMPOSIUM

The governments of Canada, Quebec and the City of Québec has the pleasure to invite you to an International Symposium for the 50th anniversary of the Food and Agriculture of the United Nations (FAO) in Québec City, Canada. The Symposium theme is **"People at the heart of Development : Food Security Through Knowledge".**

October 11-13, 1995

Spirit of the Symposium

- By emphasing food security for the world's peoples rather than the production of goods.
- By promoting know-how as the most important avenue in the search for solutions.
- By inviting both political figures and those working in the field (business and NGO's) who are determined to seek out original solutions, to meet with one another.

Three Sub-Themes

- Managing Natural Resources.
- Managing Markets.
- Managing Know-how and Technology.

Information or registration
Mr. Jean Lamontagne
FAO Symposium 1995
65 rue Sainte-Anne, Suite 100
Quebec, Québec
Tel.: (418) 691-7849
Fax : (418) 691-7815

Canada Québec :: VILLE DE québec

15th International Symposium of the North American Lake Management Society (NALMS)

Toronto, Ontario
November 6 - 11, 1995

The 15th International Symposium of NALMS will be held in Toronto, Ontario, Canada, at the Westin Harbour Castle, November 6-11, 1995. Our theme is *Aquatic Ecosystem Stewardship*. The purpose of NALMS is "to forge partnerships among citizens, scientists, and professionals to foster the management and protection of lakes and reservoirs for today and tomorrow". The Federation of Ontario Cottagers Association (FOCA) has agreed to join us in Toronto for their annual autumn meeting. FOCA has an active environment committee and a strong Lake Steward programme.

Special sessions include recovery of damaged ecosystems, lake management north of 60, preimpoundment planning of reservoir management, fish stocking as a management tool, rehabilitation and management of urban lakes and reservoirs, anoxia and phosphorus, and wetland restoration.

For further information contact

Dr. Frances Pick
telephone: 613-744-4254;
e-mail: frpick@acadvm1.uottawa.ca
or Dr. Neil Hutchinson
telephone: 705-766-2418
fax: 705-766-2254

15th International Symposium of the North American Lake Management Society (NALMS)

Toronto, Ontario
du 6 au 11 novembre 1995

Le 15^{e} symposium international de la NALMS aura lieu à Toronto (Ontario), Canada (au Westin Harbour Castle), du 6 au 11 novembre 1995. Le thème choisi est La gestion des écosystème aquatiques. Le but de NALMS est de "créer des partenariates entre les citoyens, les scientifiques et les professionnels pour encourager l'aménagement et la protection des lacs et des réservoirs pour le présent et l'avenir". La fédération ontarienne des propriétaires de chalets (FOCA) a décidé de se joindre à nous à Toronto pour tenir leur réunion annuelle de l'automne. FOCA comprend un comité environnemental très actif et un programme de Gérants des Lacs.

Quelques sessions planifiées sont la réhabilitation des écosystèmes endommagés, l'aménagement des lacs au nord du 60^{ième} parallèle, la planification des réservoirs avant inondation, la restauration et l'aménagement des lacs urbains, l'ensemencement des lacs comme outil de gestion, l'anoxie et le phosphore, et la restauration des marécages lacustres.

Pour de plus amples renseignements, communiquez avec

Frances Pick
téléphone : 613-744-4254
courrier électronique :
frpick@acadvm1.uottawa.ca
ou Neil Hutchinson
téléphone : 705-766-2418
télécopieur : 705-766-2254

1995

Annual Subscription Rates / Abonnements annuels*†‡

Publication	Volume	Code	Canada ($CAN) Institutional/ Collectif (CI)	Canada ($CAN) Personal/ Personnel (CP)	Foreign / Étranger ($US) Institutional/ Collectif (FI)	Foreign / Étranger ($US) Personal/ Personnel (FP)	Foreign / Étranger ($US) Air mail / Par avion Add / ajouter
Monthly / Mensuelle							
Biochemistry and Cell Biology / Biochimie et biologie cellulaire	73	44	242	88	242	90	75
Canadian Journal of Botany / Revue canadienne de botanique	73	45	417§	162	417§	174	150
Canadian Journal of Chemistry / Revue canadienne de chimie	73	46	477	146	477	155	150
Canadian Journal of Earth Sciences / Revue canadienne des sciences de la Terre	32	47	398	128	398	134	150
Canadian Journal of Fisheries and Aquatic Sciences / Journal canadien des sciences halieutiques et aquatiques	52	261	365	130	395	145	150
Canadian Journal of Forest Research / Revue canadienne de recherche forestière	25	54	366	119	366	123	75
Canadian Journal of Microbiology / Revue canadienne de microbiologie	41	48	279	110	279	115	75
Canadian Journal of Physics / Revue canadienne de physique	73	49	296	94	296	96	75
Canadian Journal of Physiology and Pharmacology / Revue canadienne de physiologie et pharmacologie	73	50	347	112	347	119	75
Canadian Journal of Zoology / Revue canadienne de zoologie	73	51	449	166	449	175	150
Bimonthly / Bimestrielle							
Canadian Journal of Civil Engineering / Revue canadienne de génie civil	22	52	287	92	287	97	75
Genome / Génome	38	70	262	108	262	116	75
Canadian Geotechnical Journal / Revue canadienne de géotechnique	32	53	226	88	226	95	50
Quarterly / Trimestrielle							
Environmental Reviews/ Dossiers environnement	3	244	163	57	163	63	25

*Price of regular single issues of all journals: institutional, $45.00; personal, $20.00. / Prix des numéros réguliers de toutes les revues : collectif, 45,00 $; personnel, 20,00 $.

†Rates include second-class postage. Canadian customers please include additional 7% GST (GST No. R121491807). In Quebec please add a further 6.5% QST to the total price including GST (QST No. 1006178088). / Affranchissement de deuxième classe compris. Clients canadiens veuillez ajouter 7% pour la TPS (N° de TPS R121491807). Au Québec veuillez ajouter un 6,5% de plus pour la TVQ au montant total incluant la TPS (N° de TVQ 1006178088).

‡Special rates apply for members of Canadian scientific and engineering societies if they subscribe through their respective societies. / Les tarifs spéciaux sont offerts aux membres des sociétés scientifiques et des sociétés de génie au Canada, s'ils s'abonnent par l'intermédiaire de leur société respective.

§Institutional subscriptions include a supplementary issue containing the *Proceedings of the Fifth International Mycological Congress*. / Les abonnés collectifs recevront un supplément où seront publiés les *Comptes rendus du Fifth International Mycological Congress*.

Subscriptions, renewals, requests for single or back numbers, and all remittances should be sent to Subscription Office, Research Journals, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada. Remittances should be made payable to the Receiver General for Canada, credit National Research Council of Canada.
Enquiries: Helen Goulet: 613-993-9084; Fax No.: 613-952-7656; E-mail: research.journals@nrc.ca.

Subscriptions are entered for the calendar year. There are no refunds on cancelled subscriptions once delivery has begun.

Change of address - Send change of address information (complete old address, customer code, and new address) to Subscription Office, Research Journals, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

Claims for missing numbers should be made within four months (North America) or six months (outside North America) following the date of publication. The publisher expects to supply missing numbers only when losses have been sustained in transit and when the reserve stock will permit.

Abonnements - Pour toutes les questions d'abonnements, paiements, demandes de vieux numéros de la revue, etc., on doit s'adresser au Bureau d'abonnements, Revues scientifiques, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada. Les chèques et mandats seront formulés à l'ordre du Receveur général du Canada, au crédit du Conseil national de recherches du Canada.
Renseignements : Helen Goulet : 613-993-9084; N° de télécopieur : 613-952-7656 ; Courrier électronique : research.journals@nrc.ca.

La durée des abonnements correspond à l'année civile. Les abonnements annulés ne pourront être remboursés une fois que le premier numéro sera envoyé.

Changement d'adresse - Faire parvenir tous renseignements (ancienne adresse, code du client et nouvelle adresse) au Bureau d'abonnements, Revues scientifiques, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada.

Les réclamations de numéros manquants doivent être adressées dans les quatre mois (en Amérique du Nord) ou les six mois (à l'étranger) suivant la date de publication. L'éditeur s'engage à remplacer les numéros manquants seulement lorsque les pertes ont été subies en transit et lorsque ses réserves le permettent.

Magnan, P., M.A. Rodríguez, P. Legendre, and S. Lacasse. Dietary variation in a freshwater fish species: relative contribution of biotic interactions, abiotic factors, and spatial structure **2856–2865**

Miloslavich, P., and L. Dufresne. Development and effect of female size on egg and juvenile production in the neogastropod *Buccinum cyaneum* from the Saguenay Fjord **2866–2872**

Chick, J.H., and C.C. McIvor. Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape **2873–2882**

Announcements/Avis **2883**

National Research Council Canada
Ottawa, Canada K1A 0R6

Conseil national de recherches Canada
Ottawa, Canada K1A 0R6

Postage paid at Ottawa
Publications mail
Registration pending

Port payé à Ottawa
Poste-publication
Enregistrement en cours

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques

Volume 51, No. 12, December 1994 **Volume 51, n° 12, décembre 1994**

Richards, L.J., and B.A. Megrey. Recent developments in the quantitative analysis of fisheries data 2640–2641
Kleiber, P., and J. Hampton. Modeling effects of FADs and islands on movement of skipjack tuna (*Katsuwonus pelamis*): estimating parameters from tagging data 2642–2653
Thompson, G.G. Confounding of gear selectivity and the natural mortality rate in cases where the former is a nonmonotone function of age 2654–2664
Collie, J.S., and P.D. Spencer. Modeling predator–prey dynamics in a fluctuating environment 2665–2672
McAllister, M.K., E.K. Pikitch, A.E. Punt, and R. Hilborn. A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm 2673–2687
Sampson, D.B. Fishing tactics in a two-species fisheries model: the bioeconomics of bycatch and discarding 2688–2694
Megrey, B.A., A.B. Hollowed, and R.T. Baldwin. Sensitivity of optimum harvest strategy estimates to alternative definitions of risk 2695–2704
Walters, C. Use of gaming procedures in evaluation of management experiments 2705–2714
Rosenberg, A.A., and V.R. Restrepo. Uncertainty and risk evaluation in stock assessment advice for U.S. marine fisheries 2715–2720

Hecky, R.E., P. Campbell, and D.M. Rosenberg. Introduction to Experimental lakes and natural processes: 25 years of observing natural ecosystems at the Experimental Lakes Area 2721–2722
Beaty, K.G. Sediment transport in a small stream following two successive forest fires 2723–2733
Schindler, E.U., E.R. DeBruyn, E.J. Fee, and J.A. Shearer. Sensitivity of estimates of seasonal phytoplankton photosynthesis to sampling frequency 2734–2738
Campbell, P. Phosphorus budgets and stoichiometry during the open-water season in two unmanipulated lakes in the Experimental Lakes Area, northwestern Ontario 2739–2755
Fee, E.J., R.E. Hecky, G.W. Regehr, L.L. Hendzel, and P. Wilkinson. Effects of lake size on nutrient availability in the mixed layer during summer stratification 2756–2768
Guildford, S.J., L.L. Hendzel, H.J. Kling, E.J. Fee, G.G.C. Robinson, R.E. Hecky, and S.E.M. Kasian. Effects of lake size on phytoplankton nutrient status 2769–2783
Turner, M.A., E.T. Howell, G.G.C. Robinson, P. Campbell, R.E. Hecky, and E.U. Schindler. Roles of nutrients in controlling growth of epilithon in oligotrophic lakes of low alkalinity 2784–2793
Findlay, D.L., S.E.M. Kasian, L.L. Hendzel, G.W. Regehr, E.U. Schindler, and J.A. Shearer. Biomanipulation of Lake 221 in the Experimental Lakes Area (ELA): effects on phytoplankton and nutrients 2794–2807

Fleming, I.A., B. Jonsson, and M.R. Gross. Phenotypic divergence of sea-ranched, farmed, and wild salmon 2808–2824
Hansson, L.-A., L.G. Rudstam, T.B. Johnson, P. Soranno, and Y. Allen. Patterns in algal recruitment from sediment to water in a dimictic, eutrophic lake 2825–2833
Goddard, S.V., J.S. Wroblewski, C.T. Taggart, K.A. Howse, W.L. Bailey, M.H. Kao, and G.L. Fletcher. Overwintering of adult Northern Atlantic cod (*Gadus morhua*) in cold inshore waters as evidenced by plasma antifreeze glycoprotein levels 2834–2842
Beamish, R.J., C.-E.M. Neville, B.L. Thomson, P.J. Harrison, and M. St. John. A relationship between Fraser River discharge and interannual production of Pacific salmon (*Oncorhynchus* spp.) and Pacific herring (*Clupea pallasi*) in the Strait of Georgia 2843–2855

(Continued inside back)

CJFSDX51(12)2639–2883(1994)
ISSN 0706-652X

Canada

Printed in Canada by / Imprimé au Canada par
University of Toronto Press, Inc.
Typesetting by / Typographie par
Aubut & Nadeau Services Inc.

0706-652X(199412)51:12;1-2